Effects of grazing and fire on herbaceous species in the Bolivian Altiplano

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Chapter 1

Introduction

Global change, often seen as synonymous to global warming, has many other facets, of which land use and land transformation by humans are perhaps the most severe of all. These alterations commonly lead to irreversible losses of biodiversity and soils. Human population growth and life style changes are the driver of these impacts, and intensified pastoralism is among the most widespread of causes of land destruction, particularly in poor countries.

Animal grazing changes plant communities in many ways through preference-driven biomass consumption, disturbance by trampling or dung deposition (Edwards et al., 2004). Management by humans often adds biomass cutting, weeding or burning and specific grazing regimes (Körner, 2003). Both, grazing and fire can increase the soil susceptibility to erosion but also provide open space for colonization that in turn can modify species diversity, promote seedling establishment, and change the general structure of the community (e.g. Valone & Kelt, 1999). In the Alps, moderate traditional grazing regimes with cattle and sheep commonly do not exert destructive impact on vegetation, in fact fencing cattle out from a natural pristine alpine grassland was shown to lead to a reduction of standing crop biomass by 16%, and the contribution of minor species to biodiversity was reduced (Körner, 2000). Similarly, Pucheta et al. (1998) found a decline in species richness after 4 years of fencing in montane grassland of central Argentina. So, there are sustainable grazing regimes that may actually contribute to biodiversity and ecosystem stability at high elevation. Conversely, overgrazing is known for soil compaction and increased runoff but also may massively reducing highland productivity as was shown by Tadese et al. (2003) for lower montane pastures in Ethiopia, with similar observations for many tropical highland areas. Furthermore, plants undergo characteristic adjustments of their stature when being grazed instead of being mown or remain untouched (Diaz et al., 1992). Grazing commonly leads to stunned stature, flat leaf position, fewer and smaller leaves, and apical meristems at or below the ground. Grazing also creates losers and winners among plant species, thus changing community composition. In the Tarija Altiplano in Bolivia, such effects of grazing are clearly reflected in the composition of the flora. The mechanical impact of trampling

and intensive grazing of selected plant species, led to the elimination of the most palatable, soft leaved species from certain areas, particularly close to the settlements where livestock passes daily. For instance, the swards of annual grasses of *Poa* and *Agrostis*, and perennials such as *Deyeuxia* and small species of *Festuca*, have been replaced by taller, more robust but less palatable species such as *Stipa leptostachya*, *Festuca orthophylla* and *Tetraglochin cristatum* (Beck et al., 2001). In a fencing study in the Bolivian Altiplano (3871 m), in a humid area ('bofedal'), one to three years of animal absence, surprisingly reduced plant species diversity and initiated a shift in plant species composition towards small and tall grasses dominance compared with continuously grazed sites with more forbs and sedges. In these situations, herbivory helps to reduce the height and abundance of the taller and more aggressive species thereby increasing the competitive ability of other taxa (Buttolph & Coppock, 2004). Grazing can influence fire frequency and intensity (fuel accumulation), and fire determines what is left or re-grown for herbivores, not only in terms of quantity but also in terms of forage quality (Hobbs et al., 1991). In a study by Aragon et al. (2005) in montane grasslands of NW Argentina, fire had stronger effects than grazing on biomass and plant cover, favouring more palatable species and thus also affecting species composition in the long term. It appears that the frequency of fires and grazing events is crucial for biodiversity in such high elevation grasslands.

The removal of above ground biomass by either fire or grazing or their combination can influence below ground biomass. Heavy grazing without burning led to a significantly higher root mass of 2.1 kg m^{-2} in the Colombian paramos (Hofstede and Rossenar, 1995), a remarkable effect, in view of the importance of belowground structure for soil stabilisation. On the other hand, the same authors found no difference in below ground responses in Colombian paramo grassland that was either ungrazed or grazed in combination with fire (about 1.2 kg of roots per m^2). On poorly weathered, coarse and young, often-volcanic substrate, overgrazing prevents soil stabilization and the establishment of a protective plant cover, a frequent situation in tropical highlands (Körner, 2003).

Fire is also used to re-invigorate tussock grasses (litter mineralization, induction of fresh, soft re-growth), but studies on paramo tussock vegetation showed that fire often rather leads to degradation (Laegard, 1992; Ramsay & Oxley, 1996), if the regeneration of the dominant tussock grasses takes longer than the burning intervals. Thus, burning may yield a short-term benefit, but the practice in the long term is not sustainable (Medina et al., 1997). The gain in fodder quality is

not balanced by the amount, and fires applied before plants have fully regenerated lead to plant exhaustion and losses of the mineral capital of the system.

Several of past grazing studies (see above references) were carried out in humid areas such as the paramo in the Venezuelan and Colombian Andes or the humid areas of the Peruvian and Bolivian Altiplano called 'bofedales'. However, the most extended areas in the semi-arid Bolivian Altiplano (mean height 3500 - 4000 m a.s.l.) where precipitation rarely rise above 350 mm per year, are dominated by the grassland formed by *Festuca orthophylla* tussocks ('pajonal') and associated herbaceous species. For this system, the grazing and fire impact has not yet been assessed experimentally. Moreover, the effects on ecosystem productivity and regeneration of the herbaceous species in this type of rangeland are largely unknown.

A low rate of primary productivity is one of the main reasons of the vulnerability of these ecosystems for two reasons: first, fodder shortages can become dramatic in unfavourable years, leading to massive overgrazing and second, once devastated, regeneration takes very long and may not happen without appropriate management. So both, climate variation and land use pressure contribute to variable degrees of degradation (Alzérreca, 1978). In semi-arid and arid climates the trajectory of changes following grazing removal are often unpredictable. The removal of livestock from arid grasslands or shrub lands can result in little or no change in biomass yield compared with grazed conditions for long periods (Buttolph & Coppock, 2004). In other cases, improvements in vegetation may occur under protection from grazing, but only during favourable climatic periods. A study by Alzérreca et al. (1998) reveals that changes in rangeland productivity upon release from grazing occur primarily during years of higher than average precipitation.

The herbaceous species studied here are associated with the dominant grass *Festuca orthophylla* that forms large, widely spaced tussocks. These herbaceous taxa may either grow in the gaps between tussocks (inter-tussock species) or they may be confined to the tussock (intra-tussock species) profiting from shelter and restricted animal access ('facilitation').

The aim of this thesis was to assess the role these herbaceous species play or could play in terms of biomass production and animal husbandry, in the dry grassland in the Bolivian Altiplano (Fig. A and B). Given the ongoing grazing and trampling pressure, this potential can only be explored if animals are kept away from these plants for a while. Hence, a central treatment in this project was fencing out animals. Besides exploring the effect of this protective measure, the regeneration potential was examined by assessing the seed bank. Since the absence of a ground

cover enhances erodibility the negative physical effects of poor land cover were explored in a sediment-trap experiment. Ultimately, the work should clarify the contribution of the herbaceous flora to the carrying capacity of the land, and the study should also illustrate the biodiversity effect intense grazing by camelids does exert. These questions were explored and developed in the following chapters:

Chapter 2. **Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes.** How much biomass plants invest below and above ground determines their robustness against grazing and thus, their longevity. In this chapter I explored these allometric relationships for a broad spectrum of herbaceous species from two high elevation sites in the Andes. These data should help estimating and explaining the risk of biomass losses under strong camelid grazing pressure. I had the opportunity to use similar unpublished data from NW-Argentina (4200 m a.s.l.) together with my own data from W-Bolivia (4250 m a.s.l.), with both test regions being dominated by tall *Festuca orthophylla* growing on fine volcanic substrate. This large scale comparison added to the confidence in the findings.

Chapter 3. **Herbaceous species responses to grazing and fire in the Bolivian Altiplano**. This second chapter assessed the herbaceous species responses (species richness, abundance, plant species composition and biomass production) to various experimental treatments: fenced versus non-fenced plots as the main treatment, with fire and dung addition as secondary treatments nested in the fence and non-fenced plots. I also examined the forage quality of those species in terms of N, and non-structural carbohydrates (NSC), compared to the dominant fodder plant, *Festuca orthophylla*.

Chapter 4. Soil seed bank and wind erosion in the semi-arid Bolivian Altiplano. This chapter explores the existent seed bank in the test region. I examined the differences between the seed bank in the grass puna compared to shrubland and I assessed seed vitality and vigour by germination trials and vital staining. Finally this chapter also explored the effect of land cover on wind erosion.

Chapter 5. Summarizes the outcome of this work. The final section offers a collection of the scientific posters I had offered at various conferences, as well as the colours plates of the herbaceous species I studied.

Doctoral thesis framework

This project was conducted between 2006 and 2011, with main field seasons 2007 to 2008, in the Sajama National Park, in western Bolivia at 4250 m elevation (central Andes). The work presented here was part of a study program funded by the Swiss Developmental Agency (SDC) in cooperation with the Swiss Science Foundation that also included a detailed examination of the biology and productivity of the dominant species, *Festuca orthophylla*, by Erika Hiltbrunner and José Monteiro. The work profited from cooperation with the National Herbarium of Bolivia (Stephan Beck and co-workers), the staff of the National Park and many local helpers of the farming community of Sajama village. The test area exemplifies a type of vegetation that covers vast land area in the Altiplano; hence the results apply to one of the most typical high elevation rangeland types in the tropical Andes. Low rainfall (mostly 250-350 mm per year confined to a three month rainy season), low temperatures (annual mean of 8.8 °C), volcanic ashes as substrate, and heavy grazing pressure by camelids (llamas and alpacas) and in some places sheep, are the main environmental determinants of this ecosystem.

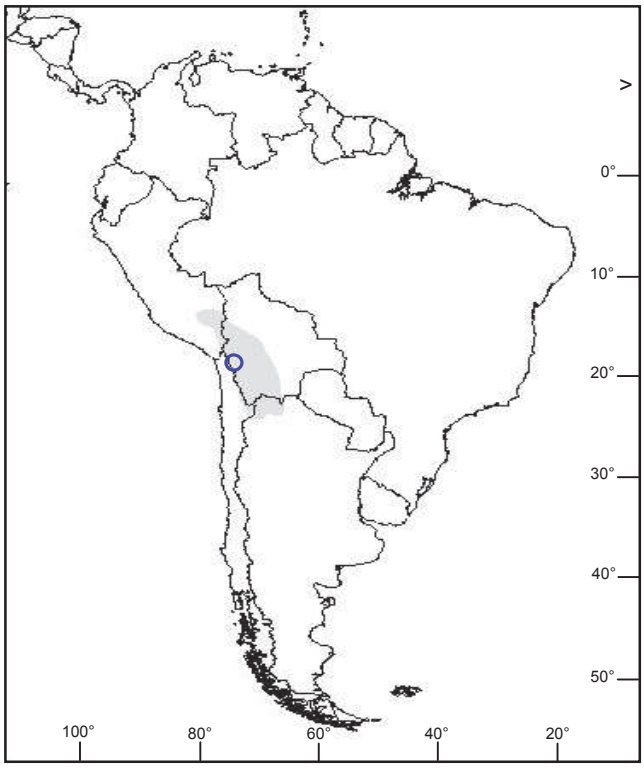

Figure A. Location of the study area in the Sajama National Park (blue circle), in the Bolivian Altiplano (grey area).

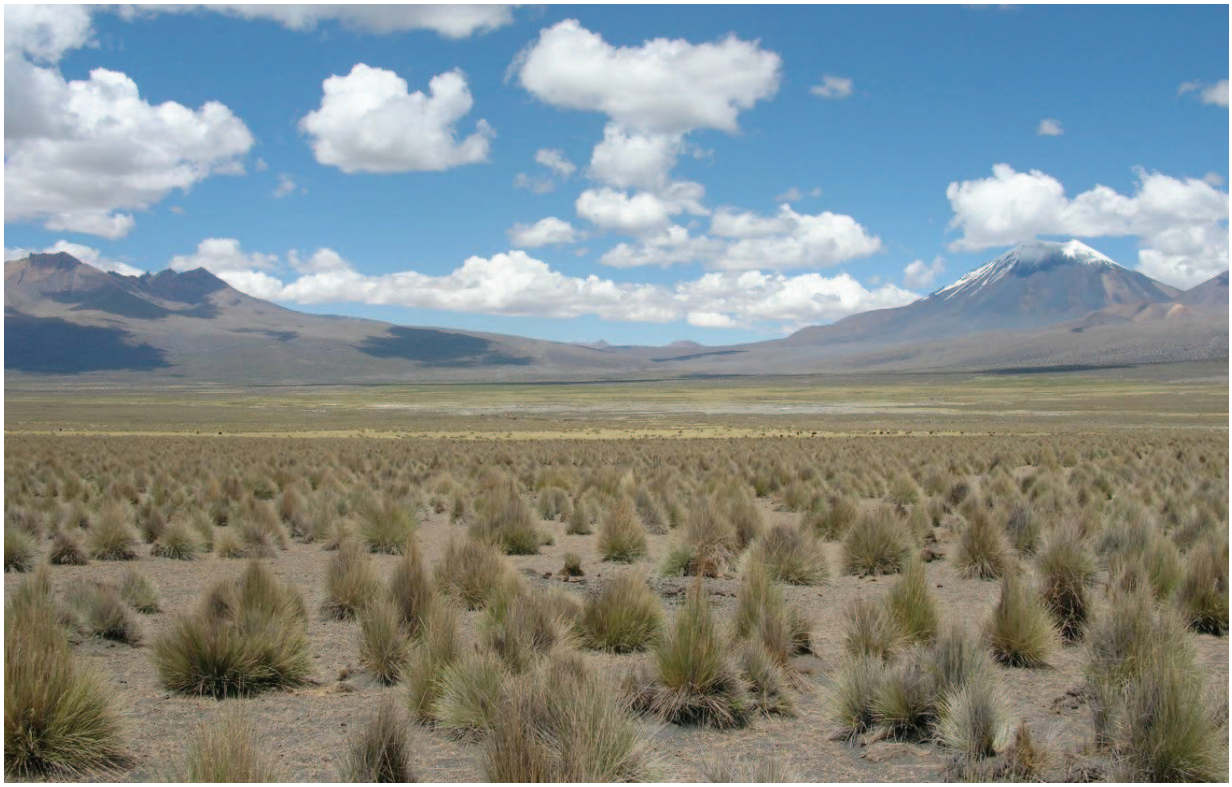

Figure B. Dry grassland dominated by *Festuca orthophylla* 'pajonal', study area at 4250 m.

Chapter 2

Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes

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Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes

Abstract

Among the plant traits that affect performance, vitality and herbivore resistance in rangeland vegetation, biomass partitioning ranks top, commonly outweighing processes at single leaves (e.g. photosynthesis, respiration). We explored the allometry of a broad sample of herbaceous species from two high elevation sites in the Andes in order to explain biomass partitioning under harsh climatic conditions and risk of biomass losses under strong camelid grazing pressure. We combined data from NW-Argentina and W-Bolivia from elevations between 4200 and 4250 m in a landscape dominated by tall *Festuca orthophylla* tussocks and a drought driven seasonality (rainfall only between November and March). Across 10 to 20 taxa per region we found less investment in leaves at these semi-arid sites and a massive below-ground storage compartment (rhizomes, tap roots), particularly at the colder Argentinean site with a mean leaf mass fraction of only 11%. Though grazing pressure was much greater in Bolivia, the foliage mass fraction was larger rather than in Argentina. The inter-tussock space in these open, dry plains ('pajonal') was dominated by rosette forming species with a below-ground shoot apex and massive tap roots (70% of all species), rendering these species less sensitive to grazing and trampling. The storage organs of these species represented more than 50 percent of total biomass. Llamas, which represented the main vertebrate herbivore in these open plains at the Bolivian site preferred non tap-root herbs and species with low leaf nitrogen concentration. Palatable forbs for llamas (22% of all species at the Bolivian site) only survived when nested (facilitated) in the rigid, tall *Festuca orthophylla* tussocks or thorny shrubs. In conclusion, these extremely high elevation rangeland herbs invested in structures for persistence (K-strategy) rather than maximizing carbon gain.

Introduction

Plant growth is driven by assimilatory and respiratory processes as well as allocation of photoassimilates to certain plant compartments. Depending on whether a compartment exerts additional carbon gain (e.g. leaves) or causes carbon costs (heterotrophic plant parts), allocation has a strong influence on overall growth (cf. Weiner, 2006). The effect of this 'investment strategy' of a plant is so large that dry matter allocation commonly outweighs the unit leaf area photosynthetic capacity as a growth determinant (Körner 2006). These relationships are explored in what has been termed 'functional growth analysis' (e.g. Poorter 1989; Van der Werf et al., 1993). Functional growth analysis considers the relative amounts of dry matter invested in certain plant compartments and the density of resultant tissues as the two major drivers of plant growth (Roy and Garnier, 1994; Lambers et al., 1998). Plant organs such as leaves, stems, reproductive organs, special storage organs, coarse, and fine roots make up total plant biomass and the investments in these compartments are best described as fractions of the total (Körner 1991, Körner 1994). The common use of ratios instead of fractions (one part divided by another part, e.g. root : shoot ratio is not advised, because it exaggerates allocation patterns and/or neglects actual function (e.g. pooling stems and leaves into 'shoot' or storage organs and fine roots into 'root' (cf. Mokany et al., 2006, for critical review of root : shoot ratios across many terrestrial biomes).

Tissue quality has successfully been expressed in density-related terms such as specific leaf area (SLA) or its reverse the leaf mass per area (LMA), and in terms of specific root length. Fast growing plants are generally found to produce a high amount of leaf area per unit dry matter (commonly thin leaves with low LMA), and also produce a great length of fine roots per unit of fine root dry matter (Ryser 1996; Poorter and Evans, 1998). While high LMA species tend to achieve longer leaf lifespan across a wide spectrum of plant functional types (Wright et al., 2002, 2004), this may not always be seen within individuals of given communities or types of species such as alpine and related lowland forb species in the European Alps (Diemer et al., 1992) but rather emerges across samples of a wider spectrum of environmental conditions. The leaf mass fraction, i.e., the total leaf mass per total plant mass and also the leaf area ratio (the total leaf area per total plant mass) are closely and positively related to plant growth rate (Poorter and Nagel, 2000).

While plant dry matter allocation is to a great part genetically determined for a given species, environmental influences can still cause significant shifts in investments towards needed structures (de Kroon et al., 2009). Evolution selects on such traits, so that species found in certain habitats exhibit certain characteristic allocation patterns (e.g. tundra plants, Bliss et al. 1980). Important drivers are life history (e.g. plant life span), light, water, nutrients, temperatures (freezing) and disturbance regimes such as grazing or fire. Water shortage (often combined with high radiation and low competition) selects for deep roots, below-ground storage organs and smaller foliage fraction in herbs and grass species (Schulze et al., 1996; Skinner et al., 2006). Disturbance resistance includes the ability to survive repeated losses of foliage by trampling, herbivory or fire and thus, also selects for large storage tissue and below-ground stems or the complete absence of above-ground stems (below-ground apices in). The alpine environment, due to its harsh climate conditions can be expected to select for certain allocation regimes (Bowman et al., 2001; Körner, 2003) and the exposure to regular disturbance may further modify dry matter allocation. Thus, biomass partitioning and biomass fractions may follow analogous patterns at high elevation (above the natural tree line) irrespective of their geographic latitudes.

In a broad survey of such characteristics in herbaceous taxa in the European Alps, Körner and Renhardt (1987) showed that roughly 24% of total plant dry matter is allocated to leaves, and, compared to comparable lowland taxa, the stem fraction is halved, whereas the root fraction is doubled. Interestingly, the leaf mass fraction did not significantly change with elevation and turned out to be a rather conservative trait across a range of cold climate regions (Körner et al., 1989; Körner, 2003). Comparable data for tropical and subtropical mountains are scarce, and the much longer growing season may favor investment strategies that differ from those in the temperate zone. Because of the absence of a dormant phase ('winter') one could expect a reduced need in storage organs, permitting greater investments in leaves and thus, an overall enhanced growth and productivity. However, much of the high altitude lands at subtropical latitudes are under the influence of high air pressure cells, leading to very low precipitation, as is the case for the semi-arid Andean Altiplano. A short growing season driven by summer precipitation in combination with low temperatures and high grazing pressure could select for even larger below-ground investments than in the temperate zone, and hence, permit only lower productivity. Therefore, we tested the following hypotheses:

(1) Biomass allocation in the cold semi-arid, subtropical regions is not different from that observed in other high elevation regions.

(2) Under similar cold life conditions increased herbivory pressure leads to more pronounced below-ground biomass allocation.

Herbivore pressure may either select for high N, short rotation foliage (low-cost, low LMA) or, more commonly for low N, high LMA, higher longevity foliage (repelling herbivores). For instance, both strategies can be found in semi-arid rangeland (e.g. Acacia *versus Combretum* strategy in the African savanna, cf. Scholes and Walker, 1993).

We hypothesized that heavy camelid pressure in combination with a cold climate and water shortage favors short rotation high N foliage. To test these hypothesis, we compared plant biomass allocation in perennial herbaceous plants growing in two semi-arid, high elevation sites in the subtropical Andes (Argentina, Bolivia) which differed mainly in grazing pressure (higher in Bolivia) but were very similar in climate conditions. The comparison across sites of similar elevation and aridity allowed some generalisations for the ecology of herbaceous plants in the high subtropical Andes as well as in a cross-continental comparison to other mountain regions of the world. Both selected sites are representing lager regions. For instance, the Altiplano covers an area of 200000 km^2, taking into account Peru, Bolivia and Argentina (Wirrmann and Mourguiart, 1995). More than the half is covered by semi-arid grasslands such as the Bolivian grassland studied here.

Material and methods

Study sites and sampling

The present study was carried out in two semi-arid sites in the subtropical Andes: one in the Cumbres Calchaquíes in NW Argentina and the other in the central Andean Altiplano (W-Bolivia; Tab. 1).

Cumbres Calchaquíes (Argentina)

The Argentinean site was in the Cumbres Calchaquíes mountains on the Huaca-Huasi plain around Laguna Nostra (26°40’ S, 65°44’ W; Halloy, 1985; Halloy and Mark, 1996; Halloy, 1998, cf. Tab. 1). This high plateau at 4200-4600 m elevation receives on average 385 mm rainfall per year (measured 1976-79, Halloy, 1985). However, more recent (but extrapolated) data indicate lower annual precipitation means between 200 and 300 mm (Bianchi et al., 1992). Rain amounts have decreased particularly since the late eighties (Bianchi et al., 2005 The mean air temperature during the main growing season (November -March) is 4.5° C, -1.6° C during the winter season, with minima down to -23° C (Halloy, 1985). The mean soil temperature at -30 cm depth is 8.1° C

in summer and -1° C in winter (Halloy, 1985). Similar climate conditions and accordingly, very comparable vegetation units (compared to the semi-arid grassland studied here) are observed over an area of 3400 km^2 (Grau 2001).

Table 1. Characteristics of the two Andean study sites

Country	Study site	Elevation [m a.s.l]	Soil type	Mean air temperature[#] [° C]	Annual Precipitation [mm]	Main grazers	Year of plant sampling
Argentina	Huaca-Huasi Cumbres Calchaquíes	4200-4600	Silty sand [a]	4.5 [a]	385 [a] 200-300[b]	Guanacos	March 1988
Bolivia	Sajama	4250	Volcanic sandy soil [c,d] Regosol [e]	8.8 [f]	327-384 [g]	Llamas Alpacas Vicuñas Sheep	March 2008

Note [#] during growing season (November-March)
Note [a] Halloy 1985
Note [b] Bianchi et al. (1992)
Note [c] Lopez et al. (2007)
Note [d] Buttolph and Coppock (2004)
Note [e] FAO (2006)
Note [f] own measurements 2003-2008
Note [g] own measurements 2006-2008

Soil moisture was surprisingly high at a depth greater than 30 cm at the time the plants were sampled (last third of the growing season, cf. Fig. 9.10. in Körner 2003). Soils in these open plains were composed of silty sands (Halloy 1985). Guanacos (wild camelid) represented the main grazers in this area, but estimates on population size of these animals are not available. Domestic grazing animals were not observed throughout several years (Halloy, personal observations) indicating that grazing pressure was relatively low at this study site.

Perennial herbs were harvested in March in 1988, close to the end of the growing season (without any visible signs of senescence; sampled by the last author in cooperation with the second author but never published). Plant cover in these open plains particularly in the inter-tussock space was very sparse, allowing to excavate individual plants almost completely (no interference by neighboring plants). However, it turned out to be near to impossible to excavate all fine roots (we assume that less than 10% of fine roots remained in the soil). Samples of 32 plant species occurring in these open plains were collected (including all existing dominant and

subdominant taxa), but abundance of single plant species varied highly, allowing replicates for 16 herb species only.

Sajama (Bolivia)

The site in the Bolivian Andes was at the western foothills of the Sajama volcano at 4250 m elevation (18°08' S, 68°58' W, Tab. 1). The growing season is clearly driven by rainfall, and lasts from December to March. Air and soil temperature were measured by means of Tidbit temperature loggers (Onset, USA); for air temperature a logger was installed at 2.80 m height above soil surface, completely screened from solar radiation. Rain measurements were taken by a rain gauge (Rainwise, USA) installed on the top of a house in the village Sajama. During the main growing season (December to March) the mean air temperature was 8.8 °C (2003-2008), the absolute minimum and maximum temperatures were -5.9 °C and 31.0 °C during this period. The mean temperature at -10 cm soil depth was 8.6 °C during the 2005/6 and 2006/7 growing seasons. The precipitation of the growing season in 2006/2007 was only 279 mm and rain set in very late (drought caused by the climatic oscillation 'El Niño'), while in the growing season 2007/2008 precipitation was 342 mm corresponding to normal seasonal rain amounts.
Thus, despite similar elevation, latitude and rainfall regime, the Bolivian site is somewhat warmer than the Argentinean site due to the intermountain location of the Altiplano which also permits tree growth (*Polylepis tarapacana*, cf. Hoch and Körner 2003, Tab. 1). Soils in the 'pajonal' consist mainly of sandy soil of volcanic origin (Lopez et al., 2007).

The Sajama National Park area (1002 km^2) is under heavy grazing pressure, largely by llamas (39000-45000) and alpacas (29000-33000), but also sheep (8000-11000) and vicuñas (3500-5000; ranges in livestock numbers result from different authors; Alzérreca, 2001; Espinoza, 2001; 'CITES', 2001). Guanacos do not occur in the Sajama region.

Plant sampling in Bolivia was carried out in mid February 2008 (peak season). We excavated 5 well developed individuals (i.e. flowering) per species in the open plains ('pajonal') covering 15 herb species which is close to the exhaustive representation of the herbaceous flora of this site. We also sampled the most abundant annual species: *Mancoa hispida*, *Tarasa tenella,* and a less abundant *Descurainea sp*. however, the data for annual species were not included in the core statistical analysis which focuses on perennials herbs. Rare species (Stephan Beck, personal communication) and graminoid species were not collected.

Plant handling

After cleaning from soil and lose debris, all plants were separated into leaves without petioles, stems (including petioles) plus reproductive organs, below-ground storage organs (root-stocks, tap roots, and all roots exceeding 2 mm in diameter), and fine root (<2 mm). In Bolivia, plant fractions were dried in a solar tent (commonly used for drying llama meat) and before weighing, the plant material was re-dried 48 h at 80° C. In Argentina, plants were first air-dried in the field and oven-dried before weighing.

For our comparison between the two Andean sites and to other mountain regions (Alps, Arctic), we used three main biomass compartments: 'leaves', 'stem', and 'below-ground'; where 'stems' also include reproductive organs (mainly flowers), and 'below-ground' includes fine roots and storage organs. 'Leaves' are defined as the photosynthetically active blade tissues only, according to functional criteria (cf. Körner, 1991, 1994). All biomass fractions (g g^{-1}) are presented on a dry weight basis.

Leaf traits

For SLA measurements (Bolivian samples only), leaves without petiole of 11 species were cut from the stem of living plants. Each leaf was cut, flattened on a mm graph paper for later reference scale, and photographed. Area was then measured analysing the digital images using the open source software ImageJ version 1.40. Leaves were dried at 80° C and weighed to calculate SLA in dm^2 g^{-1} d. w..

Leaf nitrogen

To obtain a stable mean values, leaf samples were pooled per species and ground (by ball-mill Retsch MM2000, Germany), re-dried, and N and C analyses were made by a CN analyzer (model Vario EL III, Elementar, Hanau, Germany). Leaf samples of the dominant *Festuca orthophylla* tussocks (the prime llama food) were also analysed at the Bolivian site. Green, senescent (yellow) and dead (still attached) leaves were collected from at least six individual tussocks per site, four sites within pajonal (n=4, leaf samples pooled per leaf category).

Vulnerability to grazing

The Sajama region as most of the high Andean Altiplano is a traditional pastoral zone (grazing by llama, alpaca, vicuña and sheep). We ranked the taxa collected in Bolivia by their

vulnerability to grazing in order to test whether the traits measured reflect any adaptation. Vulnerability is defined here as the risk of a plant to lose leaves by grazing or become damaged by trampling. The vulnerability to trampling was assessed both, by own observations and also by farmer's experience (interviews with local farmers). While alpaca and sheep graze the wet bofedales and the transition zones, llamas graze predominately the large, dry, open plains (dominated by *Festuca orthophylla*). When llamas graze those herbaceous plants they accept, they rarely eat the whole plant. We used the term 'medium' preference, when plants showed partial leaf loss. Preference of plants was also related to leaf N conc., leaf C/N and occurrence of tap roots.

Data analysis

Differences in total biomass, dry matter partitioning, and leaf quality (N conc. C/N ratio) between the different sampling regions were tested by analysis of variance (ANOVA) or t test. Data of biomass fraction were arcsine square root transformed prior to statistical testing. Multiple means comparisons between the two Andean sites and other mountain systems (cf. Alps, Arctic) were performed by Tukey HSD tests posterior to ANOVA. For the inter-relationships between different biomass fractions and leaf traits, data were $\log_{10}$ transformed to insure normal distribution, and tested by Pearson's product-moment correlation coefficients (r), and R^2. Plant preference by llamas was tested *versus* leaf N, C/N ratio, and occurrence of tap roots by non-parametric Mann Whitney test (medium preferred plants were also considered as accepted). The statistical analysis was made with R version 2.7.0 (www.cran.ch.r-projetct.org).

Results

Total plant biomass and biomass fractionation

There is a large variation in total plant biomass for perennial herbaceous species in both semi-arid Andean sites, ranging from 0.2 g up to >3 g (d. w.; Figure 1 illustrates typical herbaceous species occurring at the Bolivian site). The majority of the plants had a total weight of less than 1 g in dry weight. Despite the variation in total biomass, species from both semi-arid regions invested predominately in below-ground structures (> 50% of the total biomass, Tab. 2, Tab. 3, Fig. 1, 2), especially, in below-ground storage organs such as rhizomes or tap roots, but not in fine roots. In general, 'fine roots' represented the smallest of all biomass fractions. In particular, at the Argentinean site, the fine root fraction was very small (<5% of the total biomass, but probably affected by the less exhaustive digging), whereas in Bolivia it contained on average 6% of the total biomass (Tab. 2, Tab. 3).

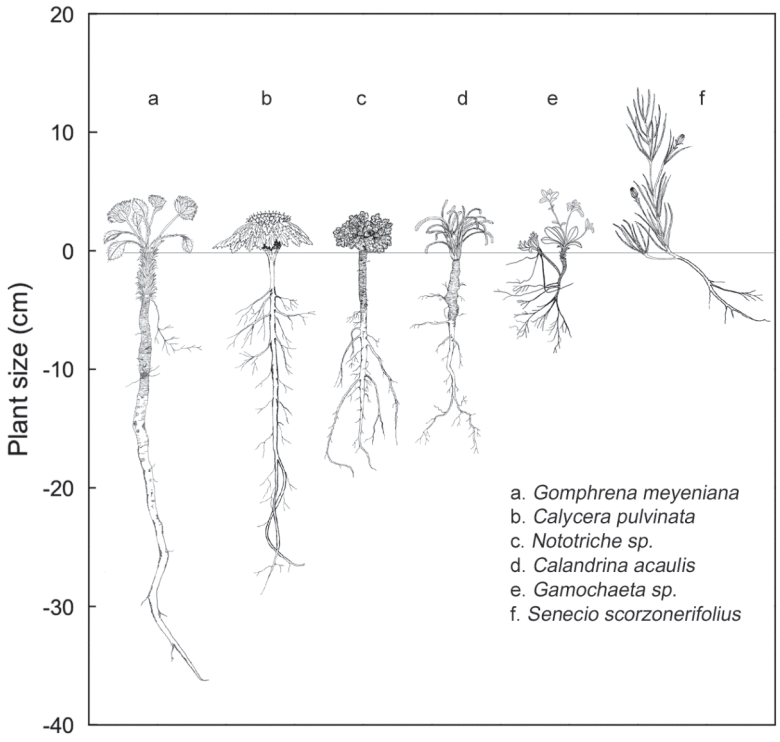

Figure 1. Typical herbaceous species in the Bolivian Altiplano

Though below-ground storage organs represented the most substantial fraction (70% of all species are tap-root species), this fraction varied strongly, ranging from 15% up to 93% of the

total biomass for the Argentinean, and between 10% and 82% for the Bolivian site (Tab. 2, Tab. 3). Less variability was seen in the leaf and in the stem fractions across all species. Plant species from Argentina had a lower mean leaf mass fraction (11%) compared to the species in Bolivia (24%; paired t-test t=3.11, *P<0.05;* Fig. 2), whereas the stem fraction (including flowers) did not differ significantly between the sites.

The allocation pattern in Bolivia was very similar to that observed in other mountain systems (Fig. 2). The predominance of biomass allocation (always > 50% of the total biomass) to below-ground structures was also seen at high alpine sites in the Austrian Alps (Fig. 2, Körner and Renhardt, 1987), also representing a near to exhaustive species representation for the given test area. In contrast to the Andean sites, the below-ground biomass in the alpine perennials in the Alps was mainly formed by fine roots (< 2 mm), with tap roots almost absent. A very similar allocation to fine roots was observed at an arctic alpine site at 69° N latitude (Fig. 2, Körner, 2003). Across all regions, the leaf mass fraction was the smallest in Argentina, reaching only half of that at all other sites. For the other regions a rather constant percentage was allocated to the leaves, contributing on average, one quarter to the total biomass (Fig. 2). By comparing the multiple means across all sites for all biomass fractions, no significant difference was found in the three biomass fractions between the two Andean sites, the sites in the Alps, and the arctic sites (ANOVA leaf fraction *F-value 1.80*, *P=0.155*; stem/flowers *F-value 1.98*, *P=0.126*; below-ground organs *F-value 0.79*, *P=0.505*).

Table 2. Total biomass (mean ± sd) and biomass fractions of perennial herbs in Argentina

Family Plant species (n)	Total Biomass	Leaves		Stem		Storage		Fine root	
	g	g	%	g	%	g	%	g	%
Fabaceae									
Astragalus sp. [a] (2)	0.43 ± 0.58	0.06 ± 0.01	16	0.21 ± 0.26	49	0.11 ± 0.09	24	0.05 ± 0.04	11
Portulacaceae									
Calandrina acaulis [a] (4)	0.64 ± 0.69	0.09 ± 0.09	15	0.10 ± 0.11	15	0.45 ± 0.49	70	0	0
***Calycera*ceae**									
Calycera pulvinata[a](14)	0.43 ± 0.30	0.18 ± 0.15	38	0.15 ± 0.12	34	0.08 ± 0.03	24	0.02 ± 0.02	4
Brassicaceae									
Draba magellanica (3)	0.06 ± 0.06	0.02 ± 0.02	47	0.01 ± 0.01	15	0.01 ± 0.01	22	0.01 ± 0.01	16
Draba sp. (2)	0.20 ± 0.10	0.04 ± 0.02	20	0.12 ± 0.07	62	0.03 ± 0.01	15	0.01 ± 0.01	2
Lepidium meyenii [a] (5)	1.74 ± 0.89	0.05 ± 0.03	3	0.06 ± 0.02	4	1.62 ± 0.85	93	0.00 ± 0.00	0
Mancoa hispida [b] (4)	0.18 ± 0.08	0.04 ± 0.02	23	0.08 ± 0.02	46	0.05 ± 0.04	27	0.01 ± 0.02	4
Geraniaceae									
Geranium sp. [a] (9)	1.04 ± 0.56	0.09 ± 0.08	9	0.11 ± 0.10	10	0.84 ± 0.46	81	0.00 ± 0.01	0
Compositae									
Perezia sp. (10)	0.25 ± 0.10	0.04 ± 0.02	15	0.03 ± 0.01	13	0.18 ± 0.08	71	0	0
Werneria heteroloba (8)	0.26 ± 0.08	0.04 ± 0.02	18	0.03 ± 0.01	14	0.18 ± 0.06	68	0	1
Hypochoeris meyeniana (7)	1.07 ± 0.51	0.11 ± 0.07	11	0.17 ± 0.10	18	0.79 ± 0.41	71	0	0
Hysterionica pulchella (3)	0.57 ± 0.44	0.06 ± 0.01	14	0.32 ± 0.31	49	0.17 ± 0.11	32	0.02 ± 0.01	5
Malvaceae									
Nototriche caesia [a] (6)	0.69 ± 0.23	0.08 ± 0.03	13	0.17 ± 0.03	26	0.41 ± 0.19	58	0.02 ± 0.01	3
Onagraceae									
Oenothera nana (2)	0.94 ± 0.21	0.17 ± 0.03	18	0.28 ± 0.24	33	0.49 ± 0.49	48	0.00 ± 0.01	1
Caryophyllaceae									
Silene sp. (6)	3.04 ± 2.14	0.13 ± 0.09	5	0.20 ± 0.13	8	2.70 ± 1.93	87	0	0
Valerianaceae									
Valeriana nivalis (2)	0.70 ± 0.09	0.11 ± 0.00	16	0.19 ± 0.10	27	0.40 ± 0.01	57	0	0
Violaceae									
Viola rodriguezii [a] (6)	0.46 ± 0.23	0.09 ± 0.03	22	0.22 ± 0.05	52	0.13 ± 0.18	23	0.01 ± 0.01	3
mean (n=16 species)	0.78 ± 0.72	0.09 ± 0.05	18	0.15 ± 0.09	28	0.54 ± 0.70	51	0.01± 0.01	3
± sd (all species)									
% of total biomass		11		19		69		1	
Non-replicated herbs									
mean (n=16 species)	0.63 ± 0.82	0.13 ± 0.11		0.16 ± 0.15		0.32 ± 0.62		0.02 ± 0.05	
± sd (all species)									
% of total biomass		21		25		50		3	

Note [a] taproot species
Note [b] annual species were not included in the main statistical analysis

Table 3. Total biomass (mean ± sd) and biomass fractions of perennial herbs in Bolivia

Family Plant species(n)	Total Biomass	Leaves		Stem		Storage		Fine roots	
	g	g	%	g	%	g	%	g	%
Fabaceae									
Astragalus pusillus [a](5)	2.64 ± 1.25	0.80 ± 0.49	28	0.44 ± 0.12	18	1.29 ± 0.70	48	0.11 ± 0.06	6
Portulacaceae									
Calandrina acaulis [a](5)	0.43 ± 0.15	0.06 ± 0.03	12	0.16 ± 0.08	37	0.20 ± 0.05	48	0.01 ± 0.00	3
***Calycera*ceae**									
Calycera pulvinata [a](5)	1.45 ± 1.01	0.38 ± 0.27	26	0.89 ± 0.67	58	0.11 ± 0.06	10	0.06 ± 0.03	6
Brassicacea									
Descurainea sp. [b] (5)	0.49 ± 0.44	0.18 ± 0.17	31	0.23 ± 0.20	45	0.04 ± 0.05	10	0.04 ± 0.02	14
Lepidium sp. [a] (5)	0.51 ± 0.44	0.13 ± 0.15	21	0.17 ± 0.10	41	0.18 ± 0.19	31	0.02 ± 0.01	6
Lepidium steinbachii [a](5)	0.61 ± 0.21	0.19 ± 0.06	31	0.21 ± 0.10	34	0.20 ± 0.08	32	0.02 ± 0.01	4
Compositae									
Gamochaeta sp. (5)	0.44 ± 0.10	0.15 ± 0.05	34	0.14 ± 0.05	31	0.08 ± 0.03	20	0.07 ± 0.10	15
Gnaphalium sp. (4)	0.67 ± 0.51	0.39 ± 0.41	50	0.11 ± 0.07	18	0.04 ± 0.01	7	0.13 ± 0.05	25
Perezia carduncelloides (5)	0.89 ± 0.22	0.11 ± 0.05	13	0.15 ± 0.02	17	0.53 ± 0.18	58	0.11 ± 0.13	12
Senecio scorzonerifolius (5)	0.91 ± 0.76	0.26 ± 0.16	32	0.19 ± 0.12	25	0.36 ± 0.49	31	0.09 ± 0.05	13
Amaranthaceae									
Gomphrena meyeniana [a] (5)	2.14 ± 0.81	0.13 ± 0.09	6	0.22 ± 0.12	10	1.74 ± 0.67	82	0.04 ± 0.04	2
Solanaceae									
Jaborosa squarrosa [a] (3)	1.08 ± 0.32	0.61 ± 0.16	57	0.22 ± 0.10	20	0.21 ± 0.11	18	0.04 ± 0.02	4
Malvaceae									
Nototriche sajamensis [a] (4)	1.14 ± 0.55	0.09 ± 0.03	8	0.14 ± 0.03	14	0.80 ± 0.52	67	0.11 ± 0.10	11
Nototriche turritella [a] (5)	2.09 ± 0.85	0.24 ± 0.11	12	0.11 ± 0.05	6	1.61 ± 0.70	75	0.14 ± 0.07	7
Nototriche sp. [a] (5)	0.35 ± 0.17	0.06 ± 0.03	19	0.10 ± 0.07	27	0.15 ± 0.07	44	0.03 ± 0.01	10
Tarasa tenella [b] (5)	0.19 ± 0.09	0.07 ± 0.03	38	0.08 ± 0.04	39	0	0	0.04 ± 0.02	22
Violaceae									
Viola rodriguezii [a] (4)	0.92 ± 0.43	0.37 ± 0.21	39	0.25 ± 0.22	25	0.24 ± 0.06	30	0.06 ± 0.03	7
mean (n=15 species) ± sd (all species)	1.08 ± 0.7	0.26 ± 0.21	27	0.23 ± 0.19	27	0.52 ± 0.56	36	0.07 ± 0.04	10
% of total biomass		24		22		48		6	

Note [a] taproot species

Note [b] annual species were not included in the main statistical analysis

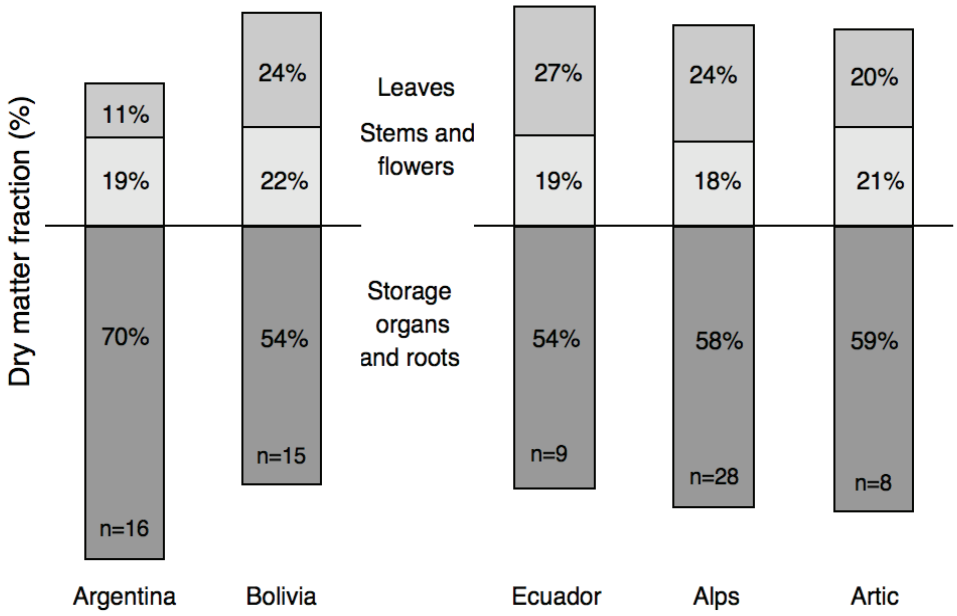

Figure 2. Biomass fractions (% of total biomass) in herbaceous plants in the semi-arid Bolivian and Argentinean Altiplano, the humid Ecuadorian Andes (unpublished data from Körner; left) compared to allocation patterns of herbaceous plants in the Alps (Körner and Renhardt 1987) and the Arctic (Prock and Körner 1996; right).

Across both Andean sites, biomass fraction of leaves was positively correlated with the stem mass (n=31, R^2=0.45, r=0.673, *P<0.001*) and to a smaller extent with the below-ground mass (R^2=0.12, r=0.349, *P=0.05*, data not shown). However, the total above-ground biomass was not related to the below-ground mass (R^2=0.11, r=0.334, n. s.). These relationships were strongly influenced by the Argentinean species. In the Bolivian species alone, leaf mass fraction was related to the stem mass (R^2=0.29, r = 0.547, *P=0.034*), but not to the below-ground biomass (R^2=0.009, r=0.095, *P=0.735*). The positive relationship between leaf and stem fraction suggests that large individuals may invest more in inflorescences.

SLA and leaf nitrogen concentration

Specific leaf area (SLA, Bolivia only) ranged between 1.0 up to > 3.0 $dm^2\ g^{-1}$with a mean value of 1.8 $dm^2\ g^{-1}$, Tab. 4). The rather high SLA value of 3.2 $dm^2\ g^{-1}$ was produced by the dense leaf rosettes of *Gamochaeta* sp.. The lowest SLA value was found in *Gomphrena meyeniana*, possibly due to the pubescence of its leaves.

Table 4. Leaf traits (mean ± sd) of perennial herbs in Bolivia

Species (number of leaves)	Leaf area (cm^2)	Leaf length (cm)	LMA $g\ dm^{-2}$	SLA $dm^2\ g^{-1}$
Astragalus pusillus (9)	0.12 ± 0.02	0.56 ± 0.05	1.08 ± 1.16	1.32 ± 0.43
Calandrina acaulis (6)	0.22 ± 0.06	1.32 ± 0.27	0.77 ± 0.08	1.31 ± 0.13
Calycera pulvinata (5)	1.78 ± 1.07	2.21 ± 0.62	0.74 ± 0.04	1.36 ± 0.07
Gamochaeta sp. (27)	0.66 ± 0.39	1.92 ± 0.79	0.33 ± 0.06	3.15 ± 0.54
Gomphrena meyeniana (18)	1.14 ± 0.50	1.49 ± 0.29	1.01 ± 0.13	1.01 ± 0.12
Jaborosa squarrosa (5)	1.41 ± 0.47	1.98 ± 0.37	0.90 ± 0.19	1.16 ± 0.24
Lepidium steinbachii (4)	0.50 ± 0.21	2.03 ± 1.02	0.37 ± 0.07	2.83 ± 0.63
Nototriche sajamensis (12)	0.44 ± 0.20	0.93 ± 0.21	0.40 ± 0.13	2.67 ± 0.62
Perezia carduncelloides (5)	1.65 ± 0.77	3.15 ± 0.54	0.54 ± 0.15	1.94 ± 0.48
Senecio scorzonerifolius (14)	0.54 ± 0.34	4.02 ± 1.77	0.54 ± 0.12	1.90 ± 0.44
Viola rodriguezzi (9)	0.10 ± 0.01	0.49 ± 0.03	0.75 ± 0.04	1.33 ± 0.07
mean ± sd (n=11)	0.78 ± 0.61	1.83 ± 1.07	0.68 ± 0.26	1.82 ± 0.75

The leaves of the Bolivian herbs had a mean N concentration of 37.6 mg g^{-1} d.w., significantly richer in nitrogen than the herbs collected in Argentina (mean of 24.9 mg N g^{-1} $P<0.001$, Tab. 5). Even when values of N_2 fixing herbs (e.g. *Astragalus*) were excluded from the data set, leaf N concentration was still by 64% higher in the Bolivian compared to the Argentinean species. In Bolivia, the highest N concentration was found in *Lepidium sp.* (51.9 mg g^{-1}), a flat rosette species growing frequently in the transition zone between the 'thola' (shrub zone) and the pajonal, whereas the lowest concentration was found in *Gamochaeta sp*. (24 mg g^{-1} N), interestingly, and in contrast to our expectation, the species with the highest SLA value (Tab. 4). Lowest N concentrations in herbs (9.7 mg g^{-1}) were comparable to the N concentration in the leaves of the dominant *Festuca orthophylla* tussocks, which are generally believed to be a poor N source for the camelids. Analysis of green *Festuca* leaves revealed a N concentration of <10 mg g^{-1} (C/N ratio 48). In senescent, yellow leaves, N concentration dropped to 2.1 mg g^{-1}.

Table 5. Leaf nitrogen concentration (mg g^{-1} d. w.) of Bolivian and Argentinean herbaceous species

Plant species in Bolivia	N mg g^{-1}	Plant species in Argentina	N mg g^{-1}
Astragalus pusillus [a]	49.1[b]	*Astragalus sp.*	37.1
Calandrina acaulis	33.8	*Calandrina acaulis*	26.7
Calycera pulvinata	43.4	*Calycera pulvinata*	42.8
Descurainea sp.	46.0	*Descurainia titicacensis*	38.7
Gamochaeta sp.	24.7	*Draba sp.*	33.8
Gnaphalium sp.	27.5	*Draba magellanica*	16.7
Gomphrena meyeniana	26.2	*Geranium sp.*	26.3
Jaborosa squarrosa	49.7	*Hypochoeris sp.*	9.7
Lepidium steinbachii	48.3	*Hysterionica pulchella*	16.2
Lepidium sp.	51.9	*Lepidium sp.*	18.8
Mancoa hispida	38.3	*Mancoa hispida*	25.6
Nototriche sajamensis	46.0	*Nototriche sp.*	39.3
Nototriche turritella	27.8	*Oenothera nana*	16.9
Nototriche sp.	29.6	*Perezia sp.*	21.2
Perezia carduncelloides	24.9	*Silene sp.*	17.8
Senecio scorzonerifolius	34.1	*Valeriana nivalis*	17.4
Tarasa tenella	36.8	*Viola rodriguezii*	26.4
Viola rodriguezii	38.3	*Werneria heteroloba*	16.7
mean ± sd (n=18)	**37.6 ± 9.5**	**mean ± sd (n=18)**	**24.9 ± 9.8**
Festuca orthophylla leaves			
green	10.0 ± 1.2		
senescent	2.1 ± 0.2		
dead	4.2 ± 1.4		

Note [a] species are ordered alphabetically (except *Festuca*)

At both sites, the leaf nitrogen concentration was positively correlated with the leaf mass fraction, i.e., the greater the leaf mass fraction the higher was the N concentration (R^2=0.14, r =0.375, *P=0.037*, data not shown). When sites were tested separately, this correlation was not statistically significant, hence, the correlation reflects a site difference. Overall, the leaf N concentration was not related to SLA values (R^2=0.05, r=-0.227, *P=0.502*).

However, tap-root herbs from the Bolivian site tended to have slightly higher leaf N concentration (40.4 ± 9.6 mg N g^{-1}; n=11) than herbs without tap root (33.2 ± 7.9 mg N g^{-1}, n=7; Mann Whitney test *P=0.093*).

Vulnerability to herbivory and plant species preferences

The tissue loss due to grazing and trampling in Bolivia varied highly from preferred to fully neglected and differed particularly between the different animal species (Tab. 6).

Table 6. Vulnerability to grazing, trampling and acceptance by different grazers of herbaceous species in the Bolivian region. Plant species are ordered along the different growing zones and by highest llama acceptance.

Species	C/N ratio	Growing zone [d]	Vulnerability [e]		Acceptance [f]		
			T	G	La	Al	Sh
Perezia carduncelloides [b]	18	Hill	High	High	A	A	A
Mancoa hispida	11	Hill	Low	Very low	N	A	A
Gamochaeta sp. [a]	17	Pajonal	High	High	A	A	A
Gomphrena meyeniana	16	Pajonal	Low	Low	M	N	N
Gnaphalium sp. [a]	15	Pajonal	High	High	A	A	A
Senecio scorzonerifolius [a]	13	Pajonal	High	High	A	A	A
Calycera pulvinata	10	Pajonal	Low	Low	M	M	M
Tarasa tenella [c]	11	Pajonal	Low	Very low	N	A	A
Jaborosa squarrosa [c]	9	Pajonal	High	Low	N	N	A
Nototriche sp.	15	Pajonal	Low	Low	N	N	N
Nototriche sajamensis	9	Pajonal	Low	Low	N	N	N
Nototriche turritella	14	Pajonal	Low	Low	N	N	N
Viola sp.	11	Pajonal	Low	Low	N	N	N
Descurainea sp.	9	Transition	Low	Low	M	M	M
Calandrina acaulis	13	Transition	High	Low	N	N	N
Lepidium steinbachii	9	Transition	Low	Low	N	N	N
Lepidium sp.	8	Transition	Low	Low	N	N	N
Astragalus pusillus	*9*	*Transition*	*Low*	*Low*	*N*	*N*	*N*

Note [a] Species facilitated only by *Festuca orthophylla*
Note [b] Species facilitated by shrubs with thorns (i.e. *Adesmia spinosissima*) and *Festuca orthophylla*
Note [c] Species growing between dung depositions, some of them can grow outside of depositions but their development is slow and rarely become a mature plant
Note [d] Growing zone pajonal (from hill to bofedal): soil moisture is assumed to be higher in hill and bofedal compared to the transition and pajonal zones
Note [e] Vulnerability to T = trampling and G = grazing
Note [f] La = Llama, Al = Alpaca and Sh = Sheep; A = accepted, M = medium, and N = not accepted.

Some of the annual species (*Tarasa, Mancoa*) were never eaten by llamas, but by alpacas and sheep; others were preferred by llamas, e.g. *Senecio scorzonerifolius*, *Gnaphalium sp.*, *Gamochaeta sp.*, *Belloa sp*., *Hypochoeris meyeniana*, and *Perezia carduncelloides*. For highly preferred species, facilitation by growing beneath or inside *Festuca* tussocks or thorny shrubs appeared to be essential (obligatory facilitation). Interestingly, species growing in llama dung deposits were fully neglected by llamas, e.g. *Jaborosa squarrosa*, *Mancoa hispida* and *Tarasa tenella*. Surprisingly, perennial species (n=15) with relatively low leaf nitrogen concentration (and therefore higher C/N ratio) were preferred by the llamas (Mann Whitney test for leaf N concentration of perennials: *P=0.018* and for leaf C/N: *P=0.017*). Tap root species forming only tiny leaf rosettes (with high N conc.) were largely rejected by llamas (Mann Whitney test *P=0.006*).

Discussion

Biomass and biomass fractionation

Overall, our data illustrate that the perennial herbaceous flora of the two semi-arid, Andean regions is characterized by small individual plant size, a high frequency of massive tap roots (70% of all species), with above-ground stems almost absent. Surprisingly, the leaf mass fraction in the heavily grazed rangeland in Bolivia was very similar to that in other parts of the world whereas in Argentina, which sees much less grazing pressure, leaf mass fraction was substantially smaller than elsewhere. Since we found an even higher proportion of below-ground storage organs at the Argentinean site with lower grazing pressure, we believe that severe freezing temperatures (lack of protection by snow cover) may be the predominant driver for the formation of such massive below-ground organs. Low annual precipitation rates may also contribute to these water storage organs. Shoot apices of most of these herbaceous, perennial species are 1-3 cm below the ground surface at both semi-arid Andean sites, thus circumventing apical freezing damage due to the harsh climate during the growing season, particularly in Argentina (Körner, 2003, Chap. 12).

The studies by Körner and Renhardt (1987), Körner (et al., 1989), Prock and Körner (1996, see Körner, 2003), unpublished data from Ecuador (cf. Fig. 2) and our study, together show a rather invariable dry matter allocation to leaves in cold high elevation habitats. Thus, leaf mass fraction seems to be a rather conservative trait, with means across representative assemblages of species commonly around 25% of the total biomass, perhaps indicating a certain critical amount

of photosynthetically active tissue needed for growth and persistence of herbaceous species in these cold habitats. The same leaf mass fraction was found here in the Bolivian species and at the by far wetter site in Ecuador, but not in the species at the Argentinean site with a mean leaf mass fraction of only 11%. In addition to the severe climatic constrains at this site, the very old age of some of these tap-rooted species may contribute to this result as some of these species may get older than 50 years (Halloy 1998, 2002). Steady accumulation of biomass to tap roots may shift the balance away from leaf matter and the live (active) fraction of these tap roots is unknown.

Across both semi-arid Andean sites, leaf mass fraction was positively related to the stem fraction (the more stem, the more leaves) and less to the below-ground biomass fraction. In plant allometry (Niklas, 1994), isometric and allometric changes of biomass fractions are distinguished. A change in size without a change in geometry or shape is a so-called isometric change, whereas a size-dependent departure of geometry, shape, etc., is an allometric change. The linear relation between the leaf fraction and the stem fraction (our data) reflects an isometric change. Such an isometric change between leaf and stem mass fraction has been shown to be valid for the majority of herbaceous species across different biomes (Niklas, 2004). However, for the below-ground biomass, our data do not match such linear scaling. The massive below-ground storage organs may be indeed very old (Halloy, 2002), whereas the leaves and stems are produced within the wet season only. Therefore, the relation between below-ground and leaf mass fractions was distorted due to the different ages of these fractions.

Leaf traits

Slow growing species found in habitats with low resource supply have been characterized by a low specific leaf area (SLA, Lambers and Poorter 1992, Poorter and Garnier 1999, Ryser 1996, Wilson et al. 1999). In alpine and arctic herbaceous plants, SLA was found to range from 1 to 3 dm^2g^{-1} with a mean of 1.8 dm^2g^{-1} (Körner et al.,1989; Prock and Körner, 1996), the very same mean was observed in the Bolivian herbs. A recent re-analysis (Jin et al., 2008) of large databases on leaf traits and metabolism rates (photosynthesis, dark respiration) of species across different biomes, re-confirmed (cf. Reich et al., 1999; Wright et al., 2004) that in stressful environments such as alpine ones, photosynthesis was closely related to SLA, but more importantly, that the slope of the relationship tended to be steeper in alpine than in more favorable habitats. This means that photosynthesis in alpine plants may be more sensitive to SLA changes, with a relatively small increase in SLA allowing a larger photosynthetic gain. Our likely

explanation is that SLA can change by either tissue density (cell wall thickness) or leaf thickness, the latter dominating alpine SLA and photosynthetic capacity (cf. Körner, 2003; Reich et al., 1998). Furthermore, pubescent leaves revealed the lowest SLA values (*Gomphrena meyeniana)* adding mass per area without photosynthetic relevance. Leaf pubescence may play a protective role under high radiation, as a buffer of fluctuating air humidity at the stomata surface, as repellent against leaf wetting, distract grazing or limit pathogen attack (Körner, 2003). SLA or its reverse LMA has been shown to be a good predictor for leaf longevity if a very broad spectrum of plant functional types is included. An extended lifespan requires a robust anatomy in form of high LMA (Reich et al., 1999; Wright et al. 2002). Diemer and co-workers (1992, Diemer et al., 1998) determined alpine leaf lifespans in perennial herbs in Austria and Ecuador, and althoug they tested herbaceous plant types only, leaf longevity was only marginally positively related to LMA and leaf longevity was relatively long (e.g. > 6 months in Ecuador). Though we did not measure leaf longevity at our Andean sites we presume a duration of < 4 months, given the short length of the humid period.

Our SLA data from the Bolivian samples were not related to leaf mass fractions nor to leaf nitrogen concentration. Llambí and co-workers (2003) noticed a decrease in SLA of the dominant species during an old-field succession in the Venezuelan Andes. They assumed that low SLA is directly associated to grazing resistance in these late successional species, not what seems to be driving the SLA at our Bolivian site, given the extremely high grazing pressure.

Leaf quality and plant preference by camelids

It is well known, that many plant species in the Andean Altiplano are toxic for camelids. For instance, *Astragalus garbancillo* has been described as very toxic to young llamas (Puch 2006). *Astragulus pusillus* in the Bolivian Altiplano showed very high leaf N concentrations, indicating that the analysis of the total leaf N concentration (rather than of specific compounds) represents a too coarse parameter for estimating food quality.

Our survey of the camelid preference for 18 different species (perennial and annual species), occurring largely in the open plains of Bolivia, revealed a preference by llamas for herbs with low leaf N concentration. We assumed that the rather high leaf nitrogen concentration in non-preferred species was presumably due to N-rich secondary compounds which may act as deterrents for llamas. Most of these nitrogen rich species formed tap roots, leading to the preference of herbs without tap roots.

In general, camelids have low demands in food quality given their main fodder is the low-nutrient *Festuca orthophylla* (Cardozo, 2007). In addition, plant selectivity of llamas may shift substantially between the wet and dry seasons (Puch, 2006; Castellaro et al., 2004). During the dry season, most of the plants are not available anymore, and llamas are forced to feed on what they get (i.e. largely on *Festuca*). In cold environments, it is often seen that the abundance of plant species rather than the number of plant species is shifted by varying grazing pressures (Sarmiento et al., 2003; Sarmiento, 2006). However, at the colder and more remote, Argentinean site more plant species were observed than at the heavily grazed Bolivian site. Sites with continuous llama grazing and breeding are described as the most degraded in terms of plant richness, but also soil stability (Podwojewski et al., 2002; Puch, 2006), thus contributing to the low plant richness in the Bolivian Altiplano. Additionally, under heavy grazing, less palatable herbs may become more abundant (Molinillo and Monasterio, 2002), whereas moderate grazing often increases plant diversity at the local or patch scale (Körner et al., 2006).

Conclusions

In the semi-arid part of the high tropical Andes, the biomass allocation of perennial herbs clearly favors massive tap roots which on average contain more than half of the total plant mass. This contrasts with findings in more humid high elevation situations elsewhere and must be related to low annual precipitation and the substantial grazing pressure at our sites. The comparison between Bolivia and Argentina suggests that severe freezing during the snowless (dry) winter adds to the selection for massive tap root formation, whereas enhanced grazing pressure (Bolivia) does not. Several herb species resist grazing by facilitation through 'hiding' in *Festuca* tussocks or by developing leaves, which, though rich in nitrogen, are not palatable to camelids. Comparing the two semi-arid regions, plant species diversity seems to decline under continuous heavy grazing pressure by camelids as shown by the reduced species richness in the *Festuca*-dominated, open plains in Bolivia, which accentuates the need for sustainable land management in these semi-arid, tropical rangelands.

Chapter 3

Herbaceous species responses to grazing and fire in the Bolivian Altiplano

Herbaceous species responses to grazing and fire in the Bolivian Altiplano

Abstract

The semi-arid Altiplano grassland is a key resource for camelid husbandry, especially in Bolivia the country with the greatest camelid number in South America. This grassland is dominated by *Festuca orthophylla* with herbaceous species playing a relatively minor role in land cover and productivity, most likely as a result of massive grazing pressure. *Festuca orthophylla* has been studied for its obvious importance as the main forage for camelids. However, the biomass production, diversity and forage quality of herbaceous species and their sensitivity to grazing and fire is largely unknown. Here we explored the responses of biomass and biodiversity to grazing pressure in these herbaceous species, using fences combined with dung addition and fire treatments. The forage quality of these herbaceous species was also examined through their nitrogen (N) and non-structural carbohydrate (NSC) cocentrations in leaves. We identified two groups of herbaceous species: The first one growing in the inter-tussock space, the second one growing inside *Festuca* (intra-tussock species) protected from grazing (facilitation). Our results show a rather depauperate ecosystem, which immediately responded to the fence. However, during our experiment, two species were alternating in dominance in the plant community during the (humid) growing season (December to March): the annual *Tarasa tenella* and the biannual *Calycera pulvinata*. These two species formed the bulk of the biomass. Dung addition favoured only *Tarasa tenella*. Fire, combined with grazing (non-fenced) showed the most destructive effect for herbaceous plants. In spite of the extremely low biomass, rather high (3x) N and NSC concentrations compared to *Festuca orthophylla*, indicates a high potential for forage improval. Our results evidence that an increase in biodiversity could enhance the carrying capacity in the semi-arid Altiplano.

Introduction

In the Andean upland puna, the presence of domesticated camelid herds dates back 6000 to 7000 years (Wheeler, 2003). These herds depend to a large extent on tussock grasses, which dominate the biomass, with small shrubs, and herbs found in the tussock interspace (Brush, 1982, Monteiro et al., 2010). This rather unique high elevation grassland ecosystem is currently exposed to disturbances such as intensive grazing and fire. While tolerating moderate grazing pressure as part of normal ecosystem functioning, recent overutilization of these grasslands enhanced erosion by wind and water, and led to weak recovery and recruitment of new tussocks as well as of herbs. It is common management practice to combine grazing with regular burning to enforce the production of more palatable, young grass shoots and to diminish necromass and litter (Verweij & Budde 1992, Hofstede et al., 1995, Ramsay 2001, Aragón et al., 2006). Burning high-altitude grasslands is performed across the entire Andean chain. In Bolivia and Peru, the fire season lasts mainly from May to October, and burning is more intense in Bolivia (Bradley & Millington, 2006). In the drier areas (i.e. outside the wet 'bofedales'), tussocks largely belong to *Festuca orthophylla*, a species that dominates almost 30% of the central Bolivian highlands (the so-called 'pajonal'). Tap-rooted perennial herbaceous genera such as *Astragalus*, *Nototriche*, *Hypochaeris*, *Calandrina*, *Gomphrena* are found in the open spaces between these tussocks (Garcia & Beck 2006, Alzérreca & Lara, 1988). These inter-tussock species are the focus of this paper.

Camelid husbandry is the economic basis of human communities, especially with llamas, because alpacas and sheep need slightly more humid conditions due to their higher forage quality requirements. Llamas are capable of living, in essence, on *Festuca orthophylla*, and their grazing behaviour supposedly does not degrade this ecosystem, provided that stocking density is not exaggerated. According to Rodríguez & Quispe (2007) sustainable camelid stocks indeed cause little damage to these semiarid grasslands, since llamas bite rather than tear their forage, and their soft, padded feet hardly impact soils. Previous works on pasture value and foraging were focussing almost exclusively on *Festuca orthophylla* (San Martín and Bryant 1989, Sequeiros 2006, Monteiro et al., 2010), whereas the role of and impact on herbaceous species remained unattended, which is surprising, given their much higher nutritional value.
Currently, camelid numbers are rapidly increasingly. Bolivia stocks c. 63% of the South American llama population (Makerman et al., 2009), and the stocking density has gone up

threefold in the last 20 years (fivefold in alpacas). In 1994 the number of llamas and alpacas was c. 711 000 and c. 87 000 respectively, and by 2004, these numbers went up to c. 2.4 million llamas and c. 417 000 alpacas (FAO, 2005). At the same time, desertification accelerated in these semi-arid regions, and 41% of the Bolivian land surface is currently considered degraded, mainly in the Altiplano (Garreaud 2001, IUCN 2001, MDSMA 1996). The consequences of the grassland degradation due to mismanagement, is a decline in biodiversity, particularly in some of the minor herbaceous plant species that are most valuable (protein-rich) fodder plants for camelids. *Festuca* forage quality is low by conventional criteria (e.g. C/N ratios), but is grazed intensively, especially by llamas (Alzérreca 2001, Genin 2002). Herbaceous species have much higher forage quality. Since these herbaceous inter-tussock species are present only during the rainy season, their availability coincides with the season of camelid births, a period, when a diet rich in protein and non-structural carbohydrates (NSC) is particularly important.

The aim of this study was to assess the effects of current land management on biomass production, biodiversity, and on the mobile pools of carbohydrates (non-structural carbohydrates, NSC) and total N concentration in foliage of herbaceous species as well as in *Festuca orthophylla* for comparative purposes. We studied the effect of: (1) grazing pressure by llamas (*Lama glama*) by exclosures, (2) pajonal burning, (3) llama dung addition, and (4) the interaction of these factors on biomass and species richness in a manipulative experiment. We hypothesized that the most destructive practice is the combination of fire and grazing.

During our study we observed one drier than normal growing season (austral summer of 2006/2007 from December to March) under the influence of 'El Niño' (ENSO) and one season (2007/2008) within the 'normal' range of precipitation 350-400 mm (Hardy et al. 1998, Vuille 1999), which is providing us with the opportunity to compare climate effects on this semi-arid and grazed ecosystem, at least, in the short term.

Material and methods

Study site

Our study area is located at 4250 m a.s.l. (18°08’ S, 68°58’ W) at the western side of the volcano Sajama (6542 m a.s.l.) in the Sajama National Park, department of Oruro Bolivia. About 150 families live in this district, with a long tradition in husbandry of llamas (53%), alpacas (39%) and sheep (8%) Alzérreca, 2001. Animal livestock is the economic basis for all families.

The growing season for inter-tussock vegetation is clearly driven by rainfall, and lasts from December to March. Air and soil temperature were measured by means of miniature temperature loggers (Tidbit, Onset, USA). For air temperature, a logger was installed at 2.80 m height above soil surface, completely screened from solar radiation. Rain measurements were taken by a dipping gauge (Rainwise, USA) installed on the top of a house in the village Sajama. During the main growing season (December to March) the mean air temperature was 8.8 °C (2003-2008), the absolute minimum and maximum temperatures were -5.9 °C and 31.0 °C during this period. In the 2006/2007 'El Niño' season, precipitation during the growing season was only 279 mm (and rain set in very late), concentrated in March (i.e. quite late), with 112 mm, while precipitation was 342 mm in the 2007/2008 growing season, i.e. close to the normal.

Soils consist of volcanic sand (86% sand, 2% silt and 12% clay), which leads to rapid surface desiccation and moisture preservation in deeper layers (no capillary continuum). In the uppermost 3 cm of the soil, the total N concentration is very low, 0.013%, and from 3 to 13 cm the total N concentration is 0.058 %, with the electrical conductivity rising from 30 µS cm^{-1} to 100 µS cm^{-1} with depth. The soil pH is slightly acidic, around 6.6. Soil moisture (vol %) was measured with sensors and a hand-held meter (EC-10 probes and ECH2O CHECK, Decagon Inc. USA) at 8-10 cm depth, in the inter-tussock soil space and under tussock canopy, both with and without llama dung, 4 sensors were installed in each place and the readings started in February 2007 ending in March 2008 (Table 2). Soil temperature was measured with two loggers (same devices as used for air temperature) buried at -10 cm, two under bare soil, one buried in the soil under a layer of llama dung. Two temperature loggers were installed directly at the raised centre of two tussocks, close to the shoot meristem zone, 5-8 cm above surrounding terrain and screened by litter and necromass. Tussock and soil loggers were exposed for almost 2 years (April 2006 to March 2008), the single logger under llama dung for one year (March 2007 to March 2008) Table 1.

Table 1. Daily minimum, mean and maximum temperature for the inter-tussock space (bare soil temperature) and within *Festuca orthophylla* tussock (Monteiro et al. 2010)

Growing season	Inter-tussock[b]			Intra-tussock[c]		
2006/2007	minimum	mean	maximun	minimum	mean	maximum
November	8.4	16.1	26.3	8.1	11.6	15.6
December	10.3	17.3	26.8	8.9	12.4	16.6
January	9.2	14.8	22.3	8.5	11.1	14.3
February	9.5	15.1	23.1	9.2	11.7	14.9
March[a]	7.7	11.5	18.6	7.3	9.1	11.6

[a] 8 days
[b] raw data were taken at -10 cm in sandy soil
[c] temperatures taken close to *Festuca* meristems under a litter of dead leaves c. 5 cm above soil.

Inter- and intra-tussock vegetation

In this study, we identified two types of non-tussock plant species: the **inter-tussock** species formed by small plants, mainly rosettes and small tussocks of graminoids growing in the gaps between the dominant tussocks of *Festuca orthophylla*; the other type of species, the **intra-tussock** species, grow nested within *Festuca orthophylla* and are herbaceous perennial plants, taking advantage from 'facilitation' by *Festuca orthophylla*. Annual or biannual herbs are largely confined to the inter-tussock area (Fig. 1).

As elsewhere in the páramo and puna (Herdberg 1979, Ramsay 1992, Bonaventura 1995), inter-tussock specie*s* are typically represented by acaulescent rosettes, with a large tap root, very short, if any, shoots and short stalked flowers. The main taxa studied in our study were *Calycera pulvinata* (*Calycera*ceae), *Mancoa hispida* (annual; Brassicacea), *Tarasa tenella* (annual; Malvaceae) and small graminoids mostly belong to scattered *Deyeuxia* tussocks, few of which ever reach the flowering stage (Poaceae; here handled as one species for the lack of inflorescences). Rare species such as *Gomphrena meyeneniana* (Amaranthaceae), and *Nototriche turritella* (Malvaceae) with only one individual each in our entire experimental area of 5000 m2, and *Urtica* sp. (Urticaceae) were not included. For a description of these taxa see Pestalozzi (1998).

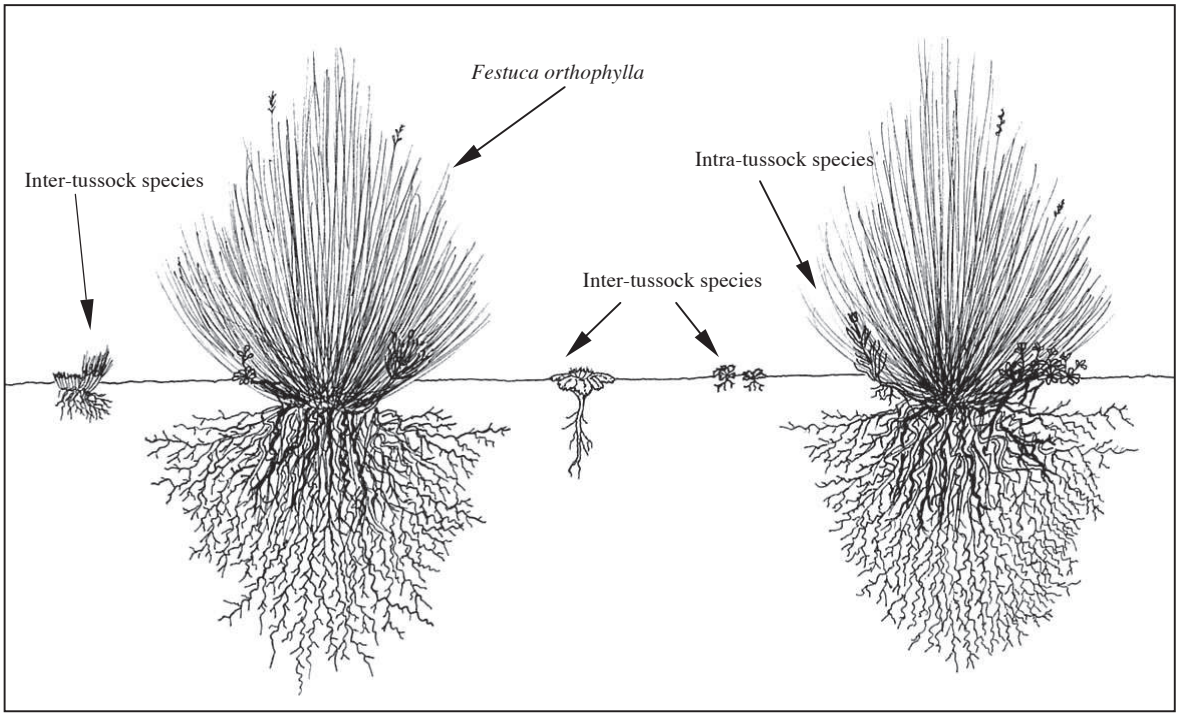

Figure 1. Inter- and intra-tussock vegetation.

Intra-tussock species are associated with *Festuca*, even in burnt plots or in dead tussocks (Fig. 2; Ramsay 1992). These herbs show morphological adjustments associated with life inside the tussocks such as slenderness, longer stems than inter-tussock herbs and protruding flowers. The main intra-tussock species all belong to the family Asteraceae, namely *Senecio scorzonerifolius*, *Gamochaeta* sp*, Belloa* sp*, Gnaphalium* sp.. When *Festuca* tussocks are burnt *Senecio scorzonerifolius* sometimes persists beneath the remaining stubble and develops to a little shrub, whereas *Gnaphalium*, *Gamochaeta* and *Belloa* become prostrate and more compact. All these species are widely spread in the Altiplano. The last three species are difficult to differentiate and our study site is dominated by *Gamochaeta* (Stephan Beck personal communication), hence, we assume all samples from this genus belong to the same species.

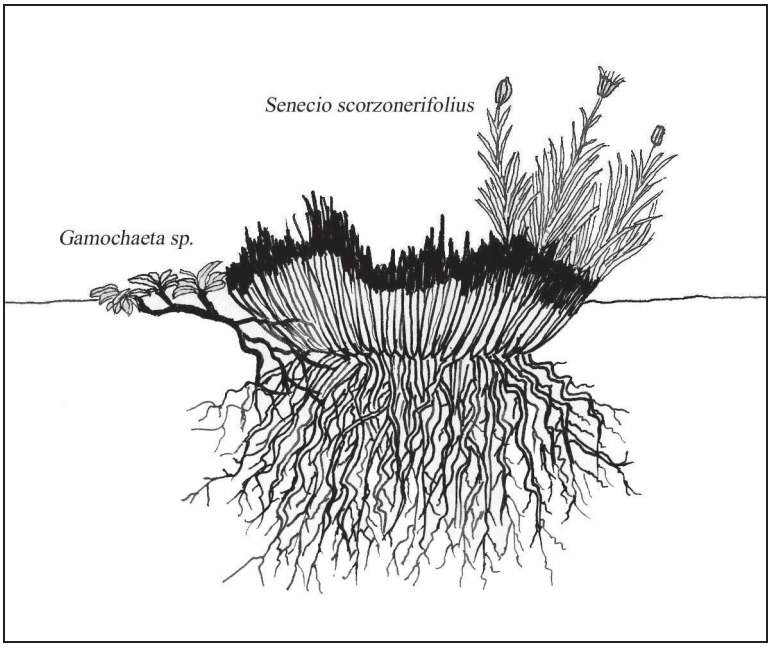

Figure 2. Dependence of intra-tussock species on *Festuca orthophylla*, even if the *Festuca* canopy is absent after burning.

Experimental design

In 2006, eight plots of 25 x 25 m (625 m^2), were established in the homogeneous dry grassland ('pajonal') of *Festuca orthophylla*, 400 m east of the edge of the village of Sajama. In order to test the effect of grazing, four plots were fenced and four were left unfenced, but boundaries were marked with wooden sticks. The eight plots were then sub-divided in four subplots where additional treatments were applied in April 2006. These were fire (all tussocks of *Festuca* were burnt in one single fire), addition of 400 L of dry llama's dung (at 1.5% total N, 0.27% P and 0.36% K, on a dry-weight basis) evenly spread on soil between *Festuca* tussocks for the next growing seasons 2006/2007 and 2007/2008, clipping of *Festuca* tussocks once to a stubble length of 10-15 cm above the ground, and control with no further treatment except for fencing and non-fencing respectively. The experimental clipping of biomass in *Festuca* was assumed not to affect the sparse herbaceous plants in the inter-tussock space; hence, this treatment was considered a duplicate control for the herbaceous species. In order to get a balanced structure of the data, we averaged the data of the two control sub-plots per plot, arriving at 4 plots. The fence is the main treatment and will be mentioned always as fence and non-fence, and additional manipulative treatments inside the plots are called treatments (nested design of the

manipulative experiment). The eight plots were set up along a very gentle slope in blocks of non-fenced and fenced plot pairs, to cover any possible block-effect in our statistical analysis that might occur across the covered slope section of c. 200 m (differences in past land use intensity, soil fertility, moisture, erosion).

Plant diversity measurements

The plant diversity in the inter-tussock space was characterized for each treatment for both years based on our census data by the Shannon-Wiener index:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

and the equitability or evenness index J

$$J = \frac{H'}{H'_{\max}} = \frac{\sum_{i=1}^{s} p_i \ln p_i}{\ln s}$$

s = the number of species; p_i = the proportion of individuals or the abundance of the ith species expressed as a proportion of total cover and ln = log $base_n$ (Kent & Coker, 1992)

Vegetation sampling

The first assessment of herbaceous species was made in February 2007 (close to the end of the exceptionally dry season, one year after set up of the experiment). We counted all plants in all plots, measured their projected ground area (maximum width and breadth converted to an ellipse), and plant height, and recorded their developmental stage in three steps: (1) vegetative, (2) flowering, and (3) fruiting. Two areas of one square meter each were randomly selected within each sub-plot (i.e. 2 in the burnt, 2 in the subplot with dung addition and 2 in each control) and all aboveground biomass was harvested. However, most of these sampling areas were empty, in part reflecting the scarcity of this vegetation, and in part, also reflecting the severe drought. We carried out a second census end of March 2008, at the end of a normal (more humid) growing season. The non-destructive census was conducted in the same way as in the year before, but, since plant density had not changed much, we did not repeat the 1 m^2 based harvests inside the experimental plots, instead we harvested a number of individual plants outside the experimental

area, and extrapolated the plot biomass by scaling observed plant size/biomass ratios (projected ground area) and overall plant density by counting all plant individuals, using allometric relationships (Niklas, 1994). We also refrained from a second destructive harvest inside our experimental area, because the treatments should be continued for several years, and treatment effects were minute, particularly during the first year. All perennial and annual plants develop their aerial parts (aboveground biomass) newly in each growing season; however, perennials accumulate their biomass in belowground storage organs formed also in previous years (Patty et al., 2010). We offer both, bulk biomass data per unit land area as well as data for the most important single species separately.

Plant biomass determination

After harvesting at least 11 complete plants of each species in the vicinity of our test area during the 2008 campaign, plants were cleaned from debris (necromass if present) and dust. Biomass was separated into green parts of leaves (the photosynthetic part, green petioles), petioles (the commonly whitish, subterrain part of petioles) together with stems (hardly any), flowers (including their stalks), storage organs and roots thicker than 2 mm, and finally, fine roots thinner than 2mm, and dried the material at 80 °C. These biomass fractions were treated for their functional attributes, rather for their anatomical nature (Körner, 1994).

Leaf N and NSC

For the assessment of non-structural carbohydrates (NSC) and leaf concentrations of N, we included *Festuca orthophylla* for comparative purposes. While we analysed mixed samples composed of green leaves from 8 well-developed plants (pooled per sub-plot) in the case of tussocks, this could not be done in the herbs, because of the scarcity of plants. For some species, individuals were not even present in all sub-plots. Except for such cases, we sampled leaves from one well-developed individual per sub-plot (n=4). All samples were dried in a solar dry-room used for drying llama meat. Before weighing, samples were dried again at 80° during 48 h in a conventional oven. Leaf samples for the chemical analyses were ground (by ball-mill Retsch MM2000, Germany) and re-dried, and analyzed with a CN analyser (model Vario EL III, Elementar, Hanau, Germany). NSC were analysed after Wong (1990) as described in Hoch and Körner (2005), using a fractionated enzymatic digest and a photometric glucose test.

Statistics

In order to test the effect of fencing and the treatments nested within fencing (subplots), a nested ANOVA model was used, where the first categorical variable was, the fence (2 levels), the explanatory and second categorical variables were the treatments in the subplots: control, dung addition and fire. Finally, each subplot was replicated in 4 plots (n=4). We also included blocks as a categorical variable. The different response variables were biomass (g m-2), Shannon index, Evenness J index, number of individuals, leaf N, NSC concentration (mg g-1) for *Festuca orthophylla* leaves. One-way ANOVA was used to compare leaf N, NSC concentration (mg g-1) of herbaceous species and Festuca, with control, fire and dung non-fenced treatments as the main effect. For the mature phenological stage of inter-tussock species we used the non-parametric Kruskal-Wallis test, given the data were not normally distributed. Changes in time were analysed by a mixed effect model. Data were transformed posterior when needed in order to normalize the data. When the main effect was significant, a Tukey HSD was used for mean comparisons, in the Kruskal-Wallis case, a Kruskal-multi-comparison was used. For the analysis of variance and posterior test we used the free software R version 2.10.0 (www.cran.ch.r-projetct.org).

Results

Microsite characteristics

Temperature in the tussock base (close to meristems) paralleled the course of soil temperature (-10 cm) in open terrain but at lower level, presumably because of shading by phytomass and litter (Monteiro, 2010, Table 1). Hence, the inter-tussock space, were the forbs grow, was a warmer environment. Soil moisture hardly ever exceeded 3 vol %, given the lack of fine pores and rapid drainage in this sandy soil. Soil moisture was nearly the same in the vicinity of tussocks and in inter-tussock space, but was higher (*P=0.02*) under the layer of llama dung (dung addition treatment; Tab. 2).

Table 2. Soil moisture (Vol %) monthly means ± sd (n=4 per area)

Year	Month	Control[1]		Fertilized[2]	
		Soil	Tussock	Soil	Tussock
2007	February	0.4 ± 0.7	-	0.6 ± 1.2	-
	March	2.4 ± 1.4	-	10.4 ± 7.0	-
	April	0.4 ± 0.6	0.5 ± 0.6	7.1 ± 5.7[a]	0.7 ± 1.3
	May	0.0 ± 0.1	0.1 ± 0.1	6.6 ± 5.2[a]	0.3 ± 0.6
	November	0.2 ± 0.4	0.1 ± 0.2	7.0 ± 6.7 [a]	0.0 ± 0.0
	December	0.0 ± 0.0	0.0 ± 0.0	4.3 ± 3.9 [a]	0.1 ± 0.2
2008	January	0.7 ± 1.0	1.6 ± 2.7	11.5 ± 8.3 [a]	1.7 ± 1.6
	February	0.5 ± 0.8	0.8 ± 1.3	8.5 ± 6.8	0.9 ± 0.8
	March	0.1 ± 0.2	0.2 ± 0.2	4.3 ± 3.0 [a]	0.5 ± 0.8

[1]Data from fenced areas, no further additional treatment
[2]Fenced and additional llama dung treatment
Letters indicate Tukey-test differences between values per month.

Plant diversity and plant cover

Overall, the species number was low, the number of individuals was extremely low, and cover was near zero when we started in 2006. There was a block-effect for inter-tussock plant number (lower numbers in the upslope blocks, *P=0.01*) and weak trends in response to the fence and the treatments (*P=0.08*, for both). Cover percent in the dry year 2007 was dominated by *Calycera pulvinata*, *Mancoa hispida* and *Deyeuxia* sp. and there was again a block effect, with lower cover upslope (Table 3) and a significant difference due to the fence but not for the additional treatments after one year. The number of species increased in 2008, and there was a block effect, a fence and a treatment effect, and the year effect (presumably due to a higher precipitation) was also significant (Table 3). Also the percent cover in the fenced and non-fenced dung treatments was higher than the other treatments in 2008, due to the greater abundance of *Tarasa tenella*. Following from the greater species number, the Shannon diversity index was also higher in 2008 than in 2007 in the fenced area (Table 3). However, the evenness index J showed only a block effect lower evenness upslope. The percent cover for intra-tussocks species was not determined.

Table 3. Means ± sd of species number, cover percent, Shannon – Winner index and J evenness index in fenced and non-fenced treatments per year, each treatment n=4.

Year	Fence	Treatment	Species	*P*	Cover %	*P*	Shannon	*P*	Evenness	*P*
2007	Non-fenced	Control	1.0 ± 0.8		0.02 ± 0.03 [A]		0.08 ± 0.09		0.03 ± 0.05	
		Fertilized	1.5 ± 1.3		0.08 ± 0.13		0.13 ± 0.16		0.12 ± 0.14	
		Fire	1.2 ± 0.9		0.00 ± 0.00 [C]		0.34 ± 0.40		0.50 ± 0.57	
				<0.01[1]		0.07[1] 0.01[2]		<0.05[1]		0.05[1]
2007	Fenced	Control	2.0 ± 1.6		0.15 ± 0.17		0.30 ± 0.34		0.30 ± 0.30	
		Fertilized	1.8 ± 1.5		0.41 ± 0.43		0.21 ± 0.32		0.19 ± 0.30	
		Fire	1.3 ± 1.3		0.38 ± 0.54		0.16 ± 0.32		0.15 ± 0.29	
				0.01[3]		<0.05[3]		0.01[3]		
2008	Non-fenced	Control	1.8 ± 1.5		0.10 ± 0.20		0.35 ± 0.50		0.46 ± 0.73	
		Fertilized	2.3 ± 0.9		0.48 ± 0.69		0.22 ± 0.19		0.25 ± 0.26	
		Fire	1.3 ± 0.9		0.03 ± 0.03 [a]		0.21 ± 0.29		0.31 ± 0.42	
				<0.001[1] <0.01[2]		<0.01[1] 0.01[2]		<0.001[1] <0.05[2]		<0.05[1]
2008	Fenced	Control	3.0 ± 2.1		0.22 ± 0.23		0.59 ± 0.44		0.43 ± 0.29	
		Fertilized	2.8 ± 1.3		1.40 ± 1.17 [bB]		0.35 ± 0.33		0.28 ± 0.24	
		Fire	2.5 ± 1.7		0.31 ± 0.36		0.59 ± 0.40		0.25 ± 0.29	

[1] difference between blocks
[2] differences between non-fenced and fenced areas
[3] difference between years
Letters mean differences between additional treatments Tukey-test (0.05)
Capital letters mean differences between additional treatments between two years

Phenology

The stages vegetative, flowering and mature (seeding) are expressed as percentage of the total number of individuals present in subplots (Tables 4 and 5). Our data reflect abundance of flowers. We cannot differentiate presence/absence of flowers due to contrasts in development or effects of grazing. The reported signals largely reflect grazing effects (removal).

Inter-tussock species

There was a clear block effect, with more flowers downslope and less flowers upslope (*P=0.05*). There was a significantly smaller fraction of individuals flowering inside the fenced control (*P=0.01*), but relatively more flowers are found in the fenced plots when combined with the dung and fire treatments in 2007 (*P=0.06*). The ratio of mature individuals was higher in dung treatment in non-fenced and fenced plots. In the more humid year (2008), the fraction of flowering individuals was slightly higher in fenced areas reciprocally the fraction of vegetative individuals lower in fenced areas. Mature individuals were almost absent in non-fenced plots

(*P=0.05*). In spite of the removal of flowers by grazing this reciprocity was maintained in non-fenced areas. However, the fraction of flowering individuals was again higher in the lower part of the slope (block effect, *P=0.01*), but also due to the fence (*P<0.05*), and the additional treatments (*P=0.01*; Table 4). There was a shift towards more flowering plants after fire in fenced plots in 2008.

Table 4. Phenological stages of inter-tussock species average of percent means ± sd (n=4)

		Non-fenced			Fenced		
Year	Stage	Control	Dung	Fire	Control	Dung	Fire
2007	Vegetative	25 ± 50	29 ± 39	63 ± 44	33 ± 46	20 ± 19	55 ± 41
	Flowering	50 ± 57	28 ± 33	4 ± 8	34 ± 40	40 ± 47	7 ± 8
	Mature	0	17 ± 23	8 ± 17	8 ± 9	15 ± 28	13 ± 15
2008	Vegetative	26 ± 34	34 ± 31	38 ± 40	24 ± 24	32 ± 46	14 ± 12
	Flowering	49 ± 44	66 ± 31	36 ± 41	50 ± 37	68 ± 46	83 ± 15
	Mature	0	0	2 ± 3	1 ± 2	0	3 ± 6

Intra-tussock species

The fraction of flowering individuals was higher downslope than upslope indicating again the block effect (Table 6). Interestingly, even intra-tussock species showed a higher fraction of flowering and mature individuals in fenced areas in 2007, indicating that the intra-tussock position was not fully protecting those herbs. This difference was only due to *Senecio* (*P<0.05*). In 2008, the higher fraction of flowering individuals in fenced plots *(P<0.01)* was largely due to *Gamochaeta* that exhibited a higher proportion of flowering individuals (*P<0.05*) than in non-fenced plots (Table 5). The block had no effect for intra-tussock species. The percentage of plants that had fruits/seeds was higher in fenced areas (*P<0.01*). The fence x treatment interaction caused flowering increases but there was a shift towards more flowering plants after fire in fenced plots in 2008 similarly to inter -tussock species (Tables 4 and 5).

Table 5. Phenological stages of intra-tussock species average of percent means ± sd (n=4)

		Non-fence				Fenced			
Year	Stage	Control	Clipped	Dung	Fire	Control	Clipped	Dung	Fire
2007	Vegetative	38 ± 48	87 ± 15	41 ± 48	83 ± 33	81 ± 17	79 ± 26	46 ± 53	52 ± 38
	Flowering	12 ± 23	13 ± 15	34 ± 45	17 ± 33	19 ± 17	21 ± 26	15 ± 19	40 ± 40
	Mature	0	0	0	0	0	0	14 ± 29	8 ± 14
2008	Vegetative	66 ± 26	33 ± 24	28 ± 21	40 ± 43	25 ± 19	36 ± 21	3 ± 5	4 ± 5
	Flowering	31 ± 27	42 ± 30	47 ± 33	60 ± 43	74 ± 19	57 ± 27	70 ± 47	89 ± 8
	Mature	3 ± 6	0	0	0	1 ± 1	7 ± 10	2 ± 2	7 ± 9

Species-specific population responses

Inter-tussock

In both years (2007 and 2008), the number of individuals per species was higher in the lower blocks ($P=0.01$; $P<0.01$, respectively; Fig. 3). In the drier year 2007, there was a positive trend in individual density in the fenced area in *Calycera* and *Mancoa* only ($P=0.05$). In 2008, the tiny *Tarasa tenella* was present in groups of hundreds due to llama dung, in non-fenced sub-plots and in fenced sub-plots with dung, indicating a fencing x dung interaction ($P<0.001$). *Tarasa* is a nitrophilous annual plant, which tends to grow almost exclusively in the vicinity of camelid dung. However, even without *Tarasa*, ANOVA revealed a significant fencing effect on the number of individuals (Fig. 3; $P=0.01$) but the fencing x dung addition interaction disappeared ($P=0.95$), which means *Tarasa* was the only species that profited from the dung treatment.

So, there is a clear positive community response to fencing, which is stronger than single species benefits. *Calycera pulvinata* shows positive response to the fence but not to the additional treatments, and the number of *Calycera* individuals was higher in 2007 than in 2008 ($P<0.01$). These differences mirror the different climatic conditions and the different species responses in the two years.

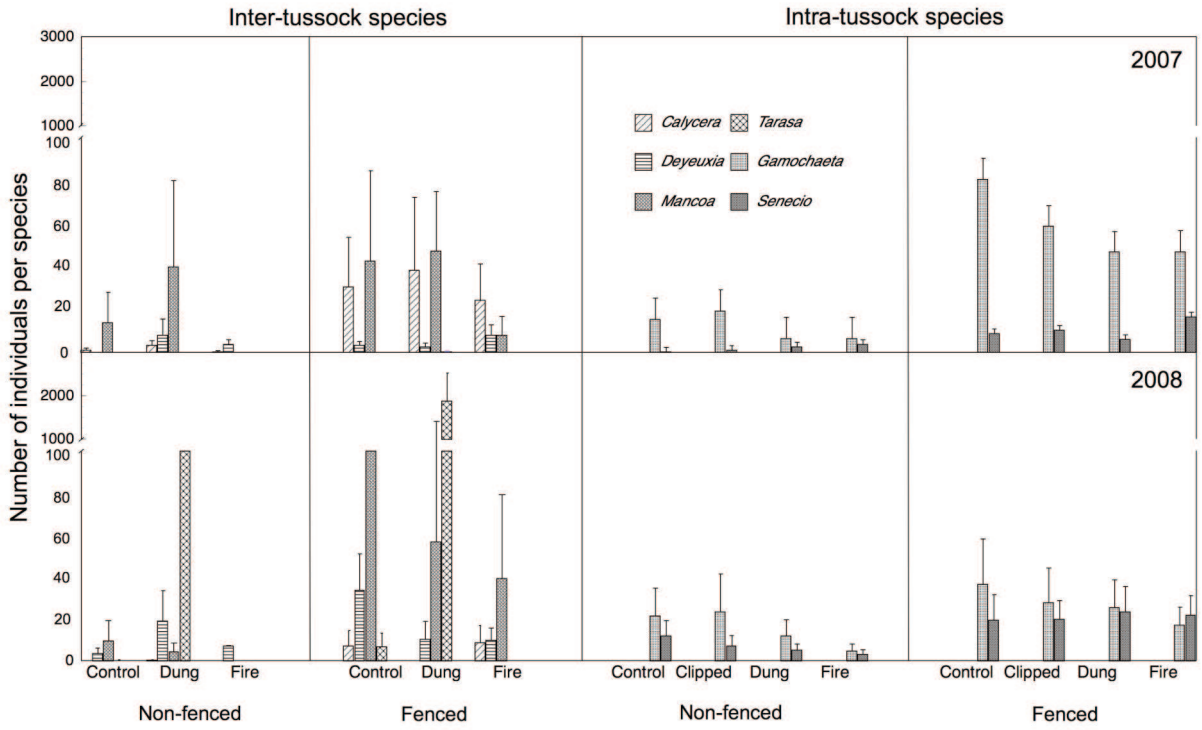

Figure 3. Number of individuals (mean + se) per species (n=4 subplots). Positive response of all species to the fence.

Intra-tussock

Very similar to the inter-tussock vegetation, the total number of individuals per intra-tussock species was lower in non-fenced treatments than in fenced treatments in both years (Fig 3, *P=0.01*). There were more individuals in 2007 than in 2008. However, this overall effect was mainly driven by *Gamochaeta* (*P=0.05*), since *Senecio* actually showed an increase in 2008 (*P=0.02*).

Biomass production

Inter-tussock above and belowground biomass

During the first (dry) growing season (2007), there was a clear fence effect, with higher total (above + belowground) biomass, compared to non-fenced plots, where the biomass was close to zero in that year (Fig. 4). Since biomass was calculated by species specific allometry data and population density per species, the community above- *versus* below-ground ratios can only change, if the fraction of taxa with specific allometries changes, which did not happen to an extent that it would change the total above- and below-ground biomass ratios due to fencing (Fig. 4, Table 6). Excluding the dominant species *Calycera pulvinata* that contributes 25% to total

biomass in non-fenced control and more than 80% in fenced control plots, ANOVA still yields a marginally significant fence effect for above and belowground biomass (*P=0.08; P=0.07,* respectively), largely caused by the grass *Deyeuxia* sp. Excluding this species from the sample, there was no trend for aboveground biomass. However, none of the species showed any effect when analysed separately.

In the second year (2008), above and belowground biomass was higher in the low part of the slope (block effect) and in fenced areas (Fig. 4). Dung addition in fenced plots increased biomass further; compared to non-fenced plots (Fig. 4, Table 6) this shows that fencing enhances the dung treatment effect (or vice versa). Excluding the annual species *Tarasa tenella* from the statistical analysis, fencing still induced a significant above and belowground increase in biomass (*P<0.05; P<0.01,* respectively).

The analysis per species showed no biomass responses for *Calycera* and *Deyeuxia* to any treatment, *Mancoa hispida* slightly increased in biomass in the fenced area (*P=0.07,* not shown). *Mancoa* was eliminated completely under fire without fence, but it survived when protected from grazing (fence x fire). *Tarasa tenella* exerted a most pronounced biomass increase under llama dung addition (*P<0.01)* for both above- and belowground biomass, but the fence-only effect was not significant, indicating that camelids hardly eat it, but trampling is likely to exert a negative effect.

Inter-tussock biomass 2007 *versus* 2008

Comparing the two years, the above-ground biomass of inter-tussock species was significantly higher in 2007 due to the different climatic conditions and fence protection (*P=0.01*). Below-ground biomass seems to be responsive to the year and the year x block effect interaction and was slightly higher in 2008, (*P=0.04*) due to the numerous and fibrous annual roots. As expected, *Mancoa* and *Tarasa* showed a significant increase in biomass in 2008 (*P<0.01*), and also the year x fence interaction was significant (*P<0.05*). *Deyeuxia* biomass increase in 2008 showed a greater year x fence interaction (*P<0.05*). There was no block effect in 2007; the positive block influence was in 2008.

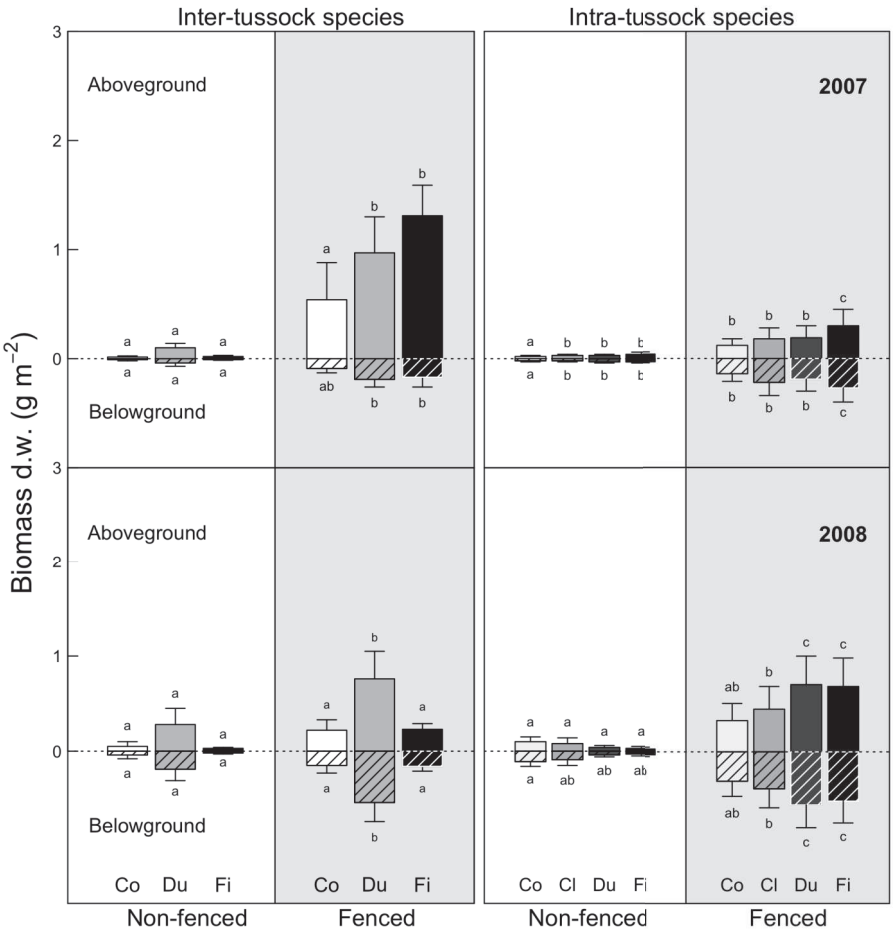

Figure 4. Above- and belowground biomass (mean + se) on a dry matter basis for non-fenced and fenced additional treatments (n=4). Different letters are significantly different according Tukey HSD (0.05). Co=control, Cl=clipped, Du= Dung, Fi= fire indicate treatments.

Intra-tussock above and belowground biomass

In 2007 above and belowground biomass of intra-tussock herbs were higher in fenced compared to unfenced plots (Fig. 4, Table 6) and there was more intra-tussock biomass in the lower part of the slope (block effect). Differences among additional treatments were significant due to the biomass increase in fire x fence treatment (Table 6). Both of the important intra-tussock species *Gamochaeta* sp. and *Senecio scorzonerifolius* profited from fencing, despite growing inside tussocks. Without the fence, their biomass was confined to the interior of the tussock. In the fenced area, plants expanded beyond the tussock periphery.

In 2008 the fence increased above and belowground biomass in intra-tussock herbs as well (Fig. 4 and Tab 6). Additional treatments also induced more biomass production (Table 6). This

overall effect is largely driven by the positive biomass response of *Senecio scorzonerifolius* (fence *P=0.04*, additional treatments *P=0.01*, data not shown), with no significant fence x additional treatments effect on *Gamochaeta* sp.

Intra-tussock biomass 2007 *versus* 2008

In intra-tussock species, above-ground and below-ground biomass was significantly higher in 2008 and more so in the fenced areas (year x fence interaction *P=0.01*). The block effect had a more positive influence on biomass production for intra-tussock species in the drier year 2007 and was not significant in 2008.

Overall our results indicate that in both years the fence enhance biomass production, the intensity of this positive response depended on plant species composition. At the same time, species dominance (composition) was mainly influenced by climatic characteristics (i.e. more precipitation more *Tarasa*, less precipitation more *Calycera*). It is worth mentioning that the biannual *Calycera* could have taken advantage of better weather conditions the previous year.

Table 6. Statistical analysis standing above and belowground biomass for inter-tussock and intra-tussock species, in 2007 and 2008

Year	Biomass	Source	df	Mean square	*F*	*P*
		Inter-tussock				
	Above-ground	Block	3	0.003	0.380	0.768
		Fence	1	0.177	22.063	0.003
2007		Fence (Treatments)	4	0.005	0.601	0.667
	Below-ground	Block	3	0.003	1.928	0.169
		Fence	1	0.041	27.711	<0.001
		Fence (Treatments)	4	0.001	0.994	0. 441
	Above-ground	Block	3	0.041	16.106	<0.001
		Fence	1	0.022	8.644	0.010
2008		Fence (Treatments)	4	0.007	2.612	0.015
	Below-ground	Block	3	0.028	10.167	0.006
		Fence	1	0.025	9.073	0.009
		Fence (Treatments)	4	0.005	1.776	0.098
		Intra-tussock				
	Above-ground	Block	3	0.006	3.186	0.019
		Fence	1	0.028	14.485	0.001
2007		Fence (Treatments)	6	0.007	3.764	0.060
	Below-ground	Block	3	0.006	3.592	0.033
		Fence	1	0.039	22.292	<0.001
		Fence (Treatments)	6	0.005	3.064	0.029
	Above-ground	Block	3	0.006	3.213	0.045
		Fence	1	0.104	52.075	<0.001
2008		Fence (Treatments)	6	0.007	3.615	0.014
	Below-ground	Block	3	0.003	1.659	0.210
		Fence	1	0.058	36.804	<0.001
		Fence (Treatments)	6	0.005	2.990	0.031

Leaf quality of herbs and Festuca

Leaves of *Festuca orthophylla* represent the main fodder for llamas; therefore we compare the N and NSC leaf concentration of the herbs to those in *Festuca.*

Herbaceous species

Compared to the hard-leaved *Festuca*, all the soft-leaved inter- and intra-tussock species exhibited a higher N concentration (from 23 to 50 N mg g^{-1}) in leaves (Table 7). Similarly, the NSC concentrations in herbaceous plants are twice as high than in *Festuca* (Fig. 5). There was also a year effect in herbs, which was due to a high starch concentration in 2007 rather than sugar. N concentration increased or decreased in a species-specific manner (Table 7). The treatments had no consistent effect. A few trends seen at the species level may reflect random effects.

Table 7. Leaf N concentration (pooled leaves per treatment)

Plant species	Treatment	2007 N mg g^{-1}	2008 N mg g^{-1}
Inter-tussock species			
Calycera pulvinata	Control	38.8	45.7 ↑
	Dung	30.2	50.1 ↑
	Fire	26.4	47.4 ↑
Deyeuxia sp.	Control	23.8	17.1 ↓
	Dung	34.8	17.4 ↓
	Fire	-	18.0
Mancoa hispida	Control	40.6	38.3 ↓
	Dung	41.4	37.3 ↓
	Fire	43.1	27.8 ↓
Tarasa tenella	Control	-	-
	Dung	32.7	44.7 ↑
	Fire	-	-
Intra-tussock species			
Gamochaeta sp.	Control	15.8	15.7
	Dung	19.4	17.1
	Fire	-	20.0
Senecio scorzonerifolious	Control	23.8	34.1 ↑
	Dung	38.6	37.3
	Fire	33.4	29.0 ↓
Festuca orthophylla			
Non-fenced	Control	10.0 ± 1.2	10.0 ± 1.4
	Clipped	14.5 ± 0.4	13.8 ± 4.9
	Dung	13.3 ± 1.2	12.3 ± 2.5
	Fire [a]	n.a.	17.1 ± 3.6
Fenced			
	Control	9.5 ± 0	10.8 ± 1.2
	Clipped	11.3 ± 1	10.3 ± 3.0
	Dung	12.3 ± 1	12.9 ± 1.4
	Fire [a]	15.9 ± 2	11.6 ± 1.2

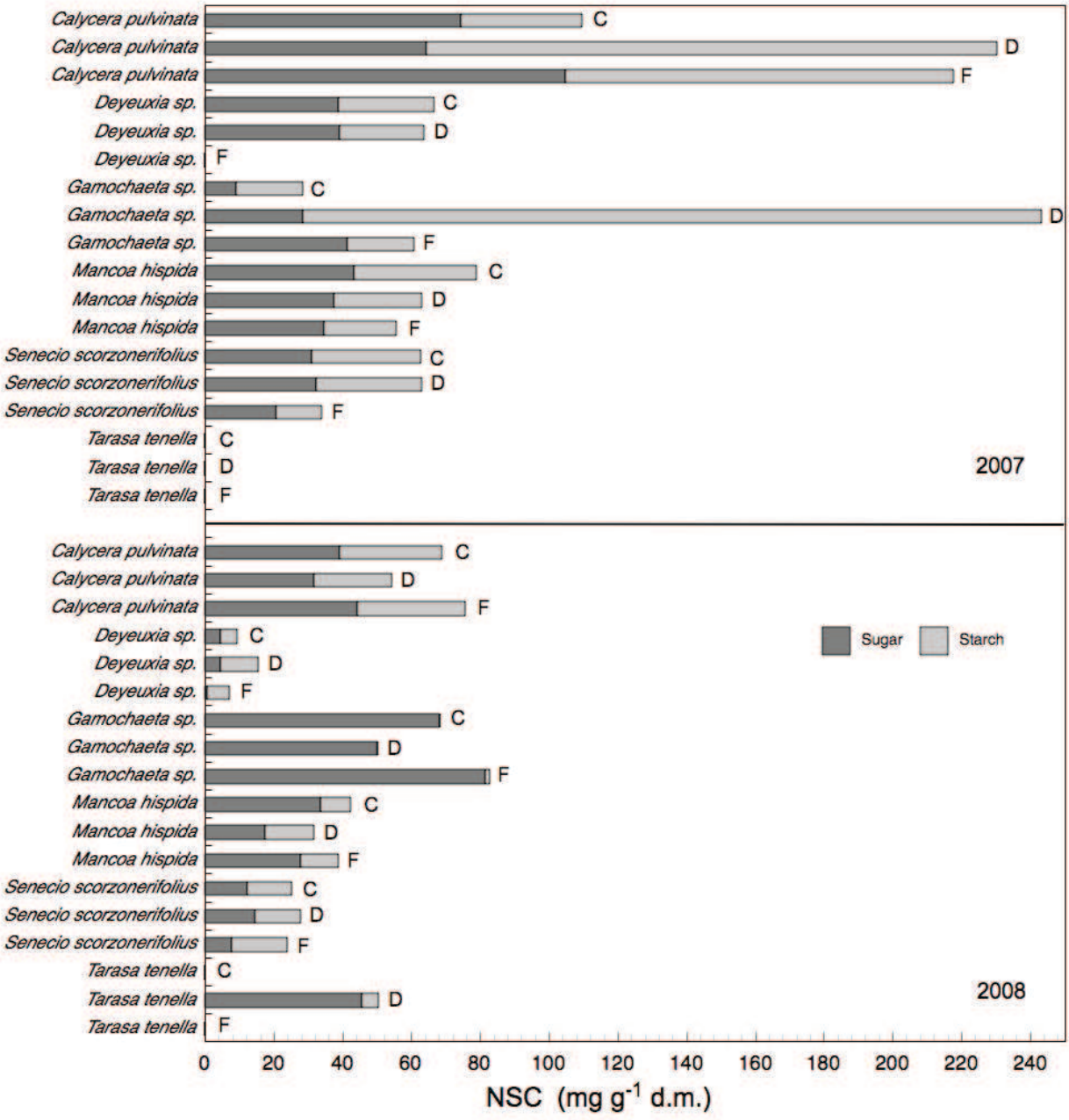

Figure 5. Non-structural carbohydrates concentration in mg g^{-1} of herbaceous species (one pooled leaf sample per species and per treatment). In 2007 and 2008: C=Control, D= Dung, F= Fire indicate treatments. In the *y* axis inter and intra-tussock species ordered alphabetically.

Festuca orthophylla

In 2007, N concentrations in mature leaves of tall *Festuca orthophylla* tussocks were in the range of 9.5 to 15.9 mg g^{-1} and the concentrations were lower in fenced tussocks (Table 7). This difference was due to the fence (Table 8). In non-fenced plots even the control showed higher N

concentration, dung and clipping treatments enhanced this difference, unfortunately we have not found any tussock leaf in the fire x non-fenced treatment due to grazing (Table 7 and 8). NSC concentrations were also higher in non-fenced than in fenced areas (Fig. 6).

Table 8. Statistical analyses for leaf quality tissue for *Festuca orthophylla* 2007 and 2008

	Variable	Source	df	Sum sq	Mean square	*F*	*P*
2007	N	Block	3	0.018	0.006	0.798	0.514
		Fence	1	0.165	0.165	21.813	<0.001
		Fence [Treatments]	4	0.152	0.007	20.121	<0.0001
	Sugar	Block	3	0.349	0.117	1.506	0.254
		Fence	1	0.131	0.131	1.695	0.212
		Fence [Treatments]	4	0.427	0.107	1.378	0.288
	Starch	Block	3	1.541	0.514	0.663	0.588
		Fence	1	0.421	0.421	0.544	0.472
		Fence [Treatments]	4	1.630	0.408	0.526	0.718
	NSC	Block	3	0.051	0.017	0.076	0.972
		Fence	1	8.108	8.108	35.926	<0.0001
		Fence [Treatments]	4	0.919	0.229	1.018	0.429
2008	N	Block	3	0.347	0.115	1.737	0.190
		Fence	1	0.294	0.294	4.425	0.047
		Fence [Treatments]	6	1.216	0.203	3.044	0.035
	Sugar	Block	3	0.409	0.136	0.389	0.761
		Fence	1	0.224	0.224	0.640	0.433
		Fence [Treatments]	6	1.549	0.258	0.736	0.626
	Starch	Block	3	0.596	0.198	2.351	0.101
		Fence	1	0.008	0.008	0.092	0.764
		Fence [Treatments]	6	0.243	0.041	0.480	0.815
	NSC	Block	3	1.167	0.389	0.923	0.446
		Fence	1	0.144	0.144	0.343	0.564
		Fence [Treatments]	6	1.768	0.295	0.699	0.653

In 2008, once more, fenced areas exhibit lower N concentrations than non-fenced areas (Table 8) and this time we found leaves in the fire x non-fenced treatment, and these necessarily young leaves showed the highest N concentration, related to their softness (Table 7). There were no differential responses in sugar and starch concentrations to any of the treatments in both years. However, sugar, and in less so starch, were significantly higher in the dry 2007 ($P=0.01$; $P<0.05$, respectively), consequently the total NSC concentration was significantly higher ($P<0.01$) in 2007 compared to 2008 across treatments (Fig. 5, table 8). Tissue re-grown after clipping was richer in NSC, presumably again because of the lower density and (softer) new foliage.

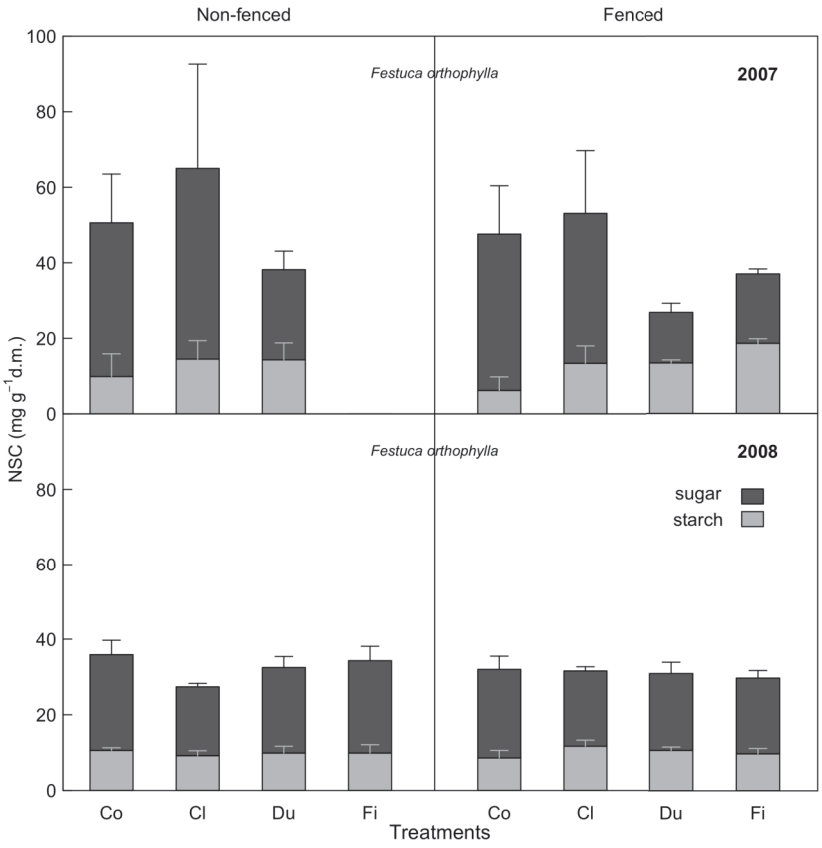

Figure 6. *Festuca orthophylla* non-structural carbohydrates (NSC) concentration in mg g^{-1} (mean + se), n=4 per treatment in non-fenced and fenced areas. Co=control, Cl=clipped, Du= Dung, Fi= fire, indicate treatments.

Discussion

This assessment of non-tussock plant biomass and species diversity in the Altiplano was faced with a rather degraded, almost deserted situation to start with. The few species other than *Festuca* tussocks that survived the high land use pressure were also present in only very few individuals, pointing at severe recruitment problems. Accordingly the herbaceous biomass and cover at the start of the experiment were near to zero. In fact, the inter-tussock plant biomass (above- and below-ground biomass) represents much less than 1% of the c. 400 g m^{-2} – 700 g m^{-2} (depending on season) of *Festuca orthophylla* biomass (Monteiro in preparation). In addition to grazing, continuous trampling makes it near to impossible for seedlings of perennial herbs to establish.

Protecting plants by fences had clearly positive effects, but given the differences in weather between the first and the second study year, it is hard to tell what is due to the better growth conditions in 2008 and what reflects the benefit of fencing. Yet, the data clearly show that llamas

remove inflorescences; hence there were more flowers when animals were kept out. Surprisingly, dung addition did not exert an overall stimulation on herbaceous growth over those two years, but rather stimulated a single nitrophilous species (*Tarasa*). The effect of dung on *Festuca* was clearly positive (Hiltbrunner et al., in preparation). But the soil moisture data suggest that this may be a mulching effect (slower desiccation), rather than a fertilizing effect, because the nutrient concentrations in the dung are extremely low. The herbaceous species left, appear to be perfectly adjusted to grazing and trampling, given that they hardly exceed a size of 5 cm and most of their biomass is closely attached to the ground (Milchunas 2002, Adler & Morales 1999). Grasses other than *Festuca orthophylla* can exceed this height (e.g. *Deyeuxia*), but only when protected against grazing (fence). Intra-tussock plants (perennial forbs) can grow taller but strongly depend on the facilitation provided by *Festuca* tussocks. In cases where the *Festuca* tussocks were burnt and not protected by a fence, intra-tussock herbs were fully removed by the grazing animals. *Senecio scorzonerifolius* and *Gamochaeta* sp. were only present when their facilitator *Festuca* was present; even in burnt tussocks, intra-tussock forbs survived below ground protected by the compact *Festuca*'s root-stock.

The current pajonal plant diversity is considered to be the product of a long history of continuous grazing combined with fire and may have eliminated certain functional or response groups or species, from the regional flora. Because perennial herb species are tap-rooted and possibly very old, any short-term changes in species diversity are only possible by the emergence of annuals. In the longer run, we expect enhanced recruitment in perennial herbs in the protected plots. In fact, three new species were identified in fenced plots (E. Beck personal observation) after four years, the inter-tussock species *Stipa brachyphylla* and intra-tussock species *Senecio dryophyllus*, even more surprising is the *Lupinus chilensis* presence, the first leguminous species in the experiment after five years, indicating that seeds of other species are arriving or are emerging from the seed banks that can contribute to a greater species richness (and herbaceous biomass) in the long run.

Non-fenced plots showed that grazing interrupted plant developmental stage. Antos et al. (1983) showed that grazing had little effect on plant reproduction if it occurred after plants had completed their seasonal life cycle. We found that the fence x dung and fire treatment interactions in 2007 and 2008 enhanced the percentage of visibly flowering individuals. Whether a longer-term effect (wave regeneration, Whelan, 2001) after fire will occur remains to be seen. Given that fire hardly affects the inter-tussock space, we doubt that such stimulation could come

into action here. Although intra-tussock forbs are severely affected by fire (a heat at the tussock base of 65 °C had been measured, compared to 500 °C in the upper canopy of *Calamagrostis* tussocks in Ecuador, (Ramsay and Oxley, 1996), they also regenerate rapidly from below-ground structures. When fenced, this leads to a significantly greater biomass, with *Senecio scorzonerifolius* even developing into abundant flowers and *Gamochaeta* forming compact, prostrate plants.

Yearly fluctuations of precipitation associated with the El Niño phenomena exert little effect on the presence/absence of long-lived, tap-rooted taxa. However, effects on annuals can be very pronounced, as was shown many times for such dry regions (Meserve et al., 2003; Gutierrez et al., 2000; Polis et al. 1997). The more severe the drought, the greater the grazing pressure on the remaining biomass. Perennials only survive by their deeply sunken apical meristems and depend on their storage reserves.

The issue of nutrient limitation in this ecosystem is not easy to resolve, given that the local taxa can be expected to be specialists for a low nutrient supply. As an indication of the rather conservative growth strategy of the forbs studied, we rather found an ephemeric species (*Tarasa*) taking advantage, not the tap-rooted perennials. According to our analysis, llama dung contained 1.5% of nitrogen, at the low end for what is known for cow dung, which (depending on fodder) can contain 1.4% - 4.2% N (NERC, 2008). This contrasts results from other, more humid regions, such as the European Alps, where even small doses of N addition increased total plant biomass (Bassin 2007, Körner 2003). According to Sala et al. (2000) nitrogen deposition in biomes that are nitrogen limited should have a large impact on biodiversity including the loss of specialized species, by favouring other more vigorous species. In our case, such a ‘winner’ is *Tarasa tenella*. A reduction of species richness under N deposition has been seen in many temperate grassland ecosystems (Bobbink 2004), but data for such semi-arid, high elevation rangeland seem to be missing.

Biomass

In the Altiplano, dung is often used for heating when firewood is scarce, N addition trough llama dung redistribution from overnight corrals is not practiced in the Altiplano. Our results showed that positive biomass responses to a dung treatment are possible, but in the short run the benefits seem to be restricted to annual herbs. Remarkably, these nitrophilous species are not widely accepted by llamas, but sheep and alpacas prefer them. Leaf quality in herbaceous species

is clearly much better in terms of protein concentration (%N), but this effect is largely the result of softer foliage, i.e. less dilution by structural biomass. Yet, animals will obtain more nutrients per unit of biomass incorporated.

Nevertheless, it seems llamas do not prefer these species – maybe the reason why they survived. Sheep and alpacas prefer at least some of the high-N species (*Tarasa* and *Mancoa*). Several Bolivian high elevation plants contain secondary metabolites such as oils and resins that may distract herbivores. Typically, plants that show high concentrations of secondary metabolites often do not employ mechanical defence such as thorns, thick cuticles or hairy leaves (Flores et al, 2004).

Green leaves from young *Festuca* individuals (small tussocks) had the highest N concentration (data not shown), ranging from 21.7 to 23.8 mg g^{-1} in fenced control sub-plots and even reach 30.5 mg g^{-1} in non-fenced control sub-plots (one homogenized sample), quite comparable to herbaceous species. NSC concentrations in such small tussocks range from 62.8 to 78.9 mg g^{-1} and, thus, are higher than in leaves of big tussocks. These high concentrations also reflect lower dry matter density of such young leaves that are commonly less sclerophyllous.

Non-structural carbohydrates are rapidly transformed into fat and milk by animals. Fructans also play an important role in Poaceae but could not be determined here. We noticed comparatively high sugar concentration in *Festuca*, with year by year variation more pronounced than in starch. Shewmaker et al. (2006) showed that sucrose was the largest contributor to NSC, in eight cultivars of tall fescue**.** In the herbaceous species examined, NSC concentrations are in the range of 40 to 80 mg g^{-1}, which is lower than in herbaceous species in the Alps, where the majority of the species contain 150 to 200 mg g^{-1}, i.e. about three times as much (Körner, 2003). The exceptionally large below-ground storage organs (Patty et al. 2010) may be one explanation, given that these structures provide a safer place to store assimilates than leaves.

Supply and demand of protein

Llamas are 58% more efficient in fodder assimilation than ovine grazers (San Martín and Bryant, 1989); this efficiency is mainly due to the ability to digest cellulose and lignin by the llama's microflora and fauna in the digestive system. According to Fowler (1998) the camelids protein requirement for an adult llama of 50 kg is 51 g day^{-1} per animal, or 8.16 g N day^{-1} per animal (6.25 conversion factor). According to Alzérreca (2001) llamas' intake is c. 1.6 kg dry matter day^{-1} from which c. 40% was *Festuca* in their study*;* the remaining 60% consisted of other

tussock grasses, herbs, grasses but also shrubs. Similarly Genin et al. (1994) found that llamas consumed between 20 - 41% of *Festuca orthophylla*.

Assuming the 8.16 g N day^{-1} per animal intake in form of *Festuca* biomass only, this would be 0.816 kg of *Festuca* dry matter day^{-1} per animal. Taking into account 400 g dry matter m^{-2} a^{-1} aboveground *Festuca* production and assuming that llamas consume only 10% of this production, one llama would need 0.74 ha day^{-1} or 274 ha a^{-1} (corresponding to a density of 0.004 llamas ha a^{-1}). The most preferred herbaceous species (*Senecio, Gamochaeta* and *Calycera*) contain a mean of 31 g N in 1 kg dry matter, which means that 260 g dry matter of herbaceous species can cover a llama's daily requirement. However, the annual plant herbaceous production is 0.05 g d.m. m^{-2} a^{-1} during three months per year (rainy season) which means, these species provide 0.0005 g dry biomass m^{-2} day^{-1}, consequently leading to 52 ha per day demand in area, to fulfill a single llamas' requirement; assuming a 100% plant herbaceous species consumption. Currently, herbaceous species could provide only 1.5% of the daily N needs by one animal in an area of 0.75 ha (for calculations of two scenarios see Annexe).

A consumption of only a 10% fraction of the total annual dry matter production of *Festuca* may be a too conservative assumption, the actual consumption is more likely bigger than 20%, and it may exceed 50% in periods of severe drought when other biomass gets scarce.

Given the only 15 % of land cover by Festuca and its low nutritional value, there is clearly a potential for increasing herbaceous biomass production and a corresponding rise in land carrying capacity. However, this requires a change in land management towards periodically protecting certain areas against fire and grazing to facilitate regeneration or for promoting the introduction of native herbaceous plants into the inter-tussock space. Given the current llamas feeding behaviour, we conclude that the high quality herbaceous fodder plants had been eradicated from this ecosystem, with only less palatable or toxic species left. This opens the option to explore the Altiplano flora for such potential fodder herbs and propagate them in nurseries for seed farming. It is also recommended to use llamas' dung to improve the soil moisture retention and to enhance the inter-tussock biomass production in the actual empty space between tussocks root spheres (which extends about 0.3 to 0.5 m from tussocks).

Overall, this study evidenced clear land use x biodiversity x productivity interactions, and the work illustrated the potential value of minor plant species in this tussock dominated, high elevation landscape. A sustainable land management that even enhances carrying capacity is not necessarily in conflict with biodiversity conservation. In fact, we see a potential for both, higher

productivity and higher biodiversity if the current overgrazing is replaced by a more controlled land use regime.

Chapter 4

Soil seed bank and wind erosion in the semi-arid Bolivian Altiplano

Soil seed bank and wind erosion in the semi-arid Bolivian Altiplano

Abstract

In semi-arid ecosystems with low plant cover and grazer presence, two factors play an important role in the dynamics of vegetation regeneration and soil protection: (1) the soil seed bank and its regenerative potential, and (2) the influence of the dominant plant species cover on soil erosion. Here we explore these questions in the 'pajonal', a semi-arid grassland dominated by *Festuca orthophylla* in the Andean altiplano (4250 m) by assessing the seedbank and sediment as well as seed translocation in response to wind and land cover. In a fencing experiment, we found that the camelids' activity (grazing and trampling) causes a significant reduction of the size of the soil seed bank, which is enhanced if combined with fire. Fencing out camelids causes the seed bank almost to double in two years. With a vital staing test using tetrazolium (TTC) we identified the most vigorous seeds, which turned out to belong to *Calycera pulvinata* and *Festuca orthophylla*. From the total grassland soil seed bank (860 seeds m^{-2}) only 17 % of all seed recovered were viable and is mainly formed by exotic seeds brought in by animal dung from the humid 'bofedales'. Our results also revealed that 'pajonal' and shrubland soil seed bank in the Altiplano is lower compared to the Bolivian prepuna shrubland. Strong winds translocate large amounts of the loose volcanic soil, including the seedbank. The presence of *Festuca orthophylla* tussocks (which on average cover only 15 % of the land) was found to reduce wind velocity by up to 62% and the *Festuca* cover diminished the amount of soil trapped in sediment traps eight fold, thus is clearly stabilizing the soil seedbed and promoting seed recruitment.

Introduction

The seed bank represents the living 'memory' of the plant community and the species present in the seed bank may include species established under previous rather than current environmental conditions, especially when severe disturbances comes into play. As such, the seed bank provides a buffer against species fluctuations and the risk of local extinction of a species and it facilitates population recovery after disturbance (Gibson, 2009). Soil seed banks have been studied because of their importance in ecosystem restoration, establishment and dynamics of vegetation succession. Several studies in semi-arid areas and deserts have shown great variability in the size and composition of seed banks in these ecosystems. Temperate grasslands are known to exhibit much larger soil seed banks compared to tropical and subtropical grasslands (Skoglund, 1992), and shrubland is also more favourable for seed conservation than grassland (Aguiar et al., 1992, Guo et al., 1998, Guo et al. 1999, Holzapfel et al. 2006). Fire and grazing can modify the size and composition of seed banks (Gonzales & Ghermandi 2008, Snyman 2005, O'Connor 1992). The duration of seed banks and their activation further depend on precipitation, wind and depth of burial (Mott 1974, Wang 1998, Guo et al. 1999, Gutterman 2000, Gutierrez and Meserve 2003).

In the Andes, the Altiplano soil seed bank is poorly known, but there is some evidence that the dry shrub puna offers favourable microhabitats for the establishment of a seed bank (Lopez, 2003). Dry Altiplano grassland that covers large areas has not yet been examined.
Given that land degradation affects 30% of Bolivia, with largest areas in the Altiplano, seed banks may be eroded before they become effective. Since grassland burning is still a common land management practice, and the fire season in May and October (Bradley and Millington 2006) coincides with periods of high wind velocity and drought, wind erosion after fire may have substantial effects on size and duration of the seed bank.

In arid and semiarid areas, soil transport and redistribution is often driven by wind (Whicker et al., 2002). Wind erosion also fundamentally depends on land-surface characteristics such as structure and degree of cover of vegetation and surface grain size (Fryrear, 1985). While soil erosion by wind is a natural process, its severity is increasing with the intensity of land use. Although not as widespread as erosion by water, the effects of wind-driven erosion are often more dramatic (White, 1997). It selectively removes nutrients and organic matter from the topsoil, including seeds. Cumulative wind erosion over many years alters soil depth and reduces

the ability of soils to store water and nutrients, with negative effects on productivity. The preservation of a seed bank during and after wind erosion may help stabilizing the land during subsequent moist periods.

In this study we assessed both the soil seed bank and a proxy of surface erosion by wind, trough the rate of sedimentation in the dry high Andean grassland ('pajonal'). We explored effects of biomass burning, grazing and land cover. As a reference, we studied the soil seed bank of adjacent shrubland. As part of the erosion studies, we also explored the amount of seeds displaced by wind in areas devoid of vegetation versus areas covered by *Festuca orthophylla*. We asked the following specific questions:

1. How does the grassland seed bank respond to burning and grazing?
2. Is the grassland seed bank different from the adjacent shrubland seed bank?
3. What is the effect of land cover on wind erosion?

Material and methods

Study site and sampling

Sajama (Bolivia)

The site in the Bolivian Andes was at the western foothills of the Sajama volcano at 4250 m elevation (18°08’ S, 68°58’ W, Tab. 1). The growing season is clearly driven by rainfall, and lasts from December to March. Air and soil temperature were measured by means of Tidbit temperature loggers (Onset, USA); for air temperature a logger was installed at 2.80 m height above soil surface, completely screened from solar radiation. Rain measurements were taken by a rain gauge (Rainwise, USA) installed on the top of a house in the village Sajama. During the main growing season (December to March) the mean air temperature was 8.8 ° (2003-2008), the absolute minimum and maximum temperatures were -5.9° C and 31.0 °C during this period. The mean temperature at -10 cm soil depth was 8.6 °C during the 2005/6 and 2006/7 growing seasons. The precipitation of the growing season in 2006/2007 was only 279 mm and rain set in very late (drought caused by the climatic oscillation 'El Niño'), while in the growing season 2007/2008 precipitation was 332 mm corresponding to normal seasonal rain amounts. During winter months, conditions over the Altiplano are usually dry, in association with strong and steady westerly and northwesterly winds over the entire region (Vuille, 1999). Vegetation is characterized by *Polylepis tarapacana* (Queñua) confined to rocky slopes, three shrub species;

Bacharis incarum, Parastrephia lepidophilla, *Parastrephia quadrangularis, Bacharis boliviensis* (Thola) and the tussock *Festuca orthophylla* (paja brava).
The Sajama National Park area (1002 km^2) is under heavy grazing pressure, largely by llamas (39000-45000) and alpacas (29000-33000), but also sheep (8000-11000) and vicuñas (3500-5000); Alzérreca 2001; Espinoza 2001; CITES 2001.

The experiment

In March 2008, at the end of the wet 'summer' season, soil seed bank samples were collected within an experimental area with fencing (± grazing) and fire treatments. Eight plots (625 m^2 each) were set up in the homogeneous 'pajonal' dominated by *Festuca orthophylla*, 400 m east of the edge of the village of Sajama in 2006. Four plots were fenced and four were left unfenced and thus grazed, with boundaries marked. The eight plots were sub-divided in four parts where additional treatments were applied. These were: fire (all tussocks of *Festuca* were burnt); fertilization with 400 L dry llama's dung; simulated grazing (tussocks of *Festuca* cut), and control. Since the clipping treatment does not affect the inter-tussock space, this treatment was considered a duplicate control plot for the current purpose. In order to get a balanced structure of the data, we averaged the data of the two controls, arriving at 4 plots. We did not make any use of the dung addition treatment in this study. Thus, our treatments include non-fenced and fenced, fire and control (no fire, no fence). Simultaneously four plots of 156 m^2 each were established in the shrubland next to the 'pajonal', to compare the differences of seed quantities between open controls 'pajonal' versus shrubland.

Soil sampling

In February 2008, soil samples were collected to know the substrate characteristics of our study areas, for grassland and also shrubland, we collected six samples of the first 3 cm top soil and also six samples at 10 cm depth, then were homogenized and pH, electrical conductivity and soil texture were analysed at PROMIC (Programa de Manejo Integrado de Cuencas) in Bolivia.

Percent cover of vegetation

To determine the percent vegetation cover we used ropes to outline two strips of a meter width each, one placed longitudinally and the other transversally in each treatment. The strips were subdivided every meter and the percentage of plant cover (in essence *Festuca* cover) was estimated visually.

Soil seed sampling and handling

In all plots we set up a 3 m grid for sample collection. Sampling was obtained at each grid point using a metallic cylinder corer of 5 cm in diameter and 5 cm deep. At this stage we distinguished two samples: the first taken in the open space between tussocks or shrubs and the second taken from the soil right beneath shrub or tussock plants next to the nearest grid point. Each sample was stored in paper bags and dried at ambient temperature for a week. Then the organic material was separated from the soil trough flotation in water and dried at 20 °C, at the National Herbarium of Bolivia 6 months after collection. Seeds were separated from the organic material using a stereoscope; entire seeds were selected for later seed viability analysis and weighed.

Seed vitality

We employed a tetrazolium test (ISTA 2006) to determine live seed tissue. We immersed seeds in colorless solution of 2,3,5-triphenyl tetrazolium chloride as an indicator for the biochemical reduction potential within living cells (TTC is an acceptor of hydrogen from the dehydrogenases). By hydrogenation, TTC turns into red triphenyl formazan, which remains tied to living cells. In order to ensure TTC penetration we analysed older Sajama's seeds (2007), including *Calycera pulvinata* (ripe fruit) and *Jaborrosa squarrosa* having the thickest testa. We cut the seeds to observe TTC penetration and both seeds showed an intense red colour. This way we distinguished red-coloured living parts of seeds from the colourless dead ones in a microscope.

After the microscopic TTC analysis, the seeds were submerged in 1 ml ethanol (at 96%) and left for 15 minutes in a water bath at 85 °C. After cooling, another 1ml of ethanol (96%) was added, and the extraction solution was analyzed in a photometer (Spectrophotometer serie10 UV, Genesys^{TM}, made in USA calibrated at 530 nm). The difference between the maximum (0.030) and minimum (0.018) value obtained (tested in *Calycera pulvinata*) in a photometric analyze was

the reference range (0 - 100%) for determining the percentage of live seeds (vigour) in the seed collection. A seed was considered viable when its TTC signals exceed or was equal to 50% of the *Calycera* reference signal.

Wind velocity

Erosion studies were conducted in two larger areas: one with *Festuca* cover and the other one an open terrain of ca. 200 m^2 without any vegetation. The whole terrain was flat. Wind velocity was measured with 7 anemometers (Windmaster 2, ©Kaindl electronics, made in Germany) that registered the average and the maximum value in m s^{-1}. One anemometer at 155 cm height served as control, three were placed among *Festuca* tussocks at 75 cm, 40 cm and 10 cm above ground; a second set of three anemometers was placed at the same height in the centre of the bare soil area. Two measurement campaigns were conducted, one in summer (rainy season) on 18 and 27 February with all 7 anemometers as described above, and one in winter (on 25, 27, 29 and 31 August), this time only the anemometers at 155 and 40 cm above ground, the best in both test areas.

Sediment collection with dust traps

To collect sediment, dust traps were built from half litre PET bottles, cut at 15 cm height to prevent losses of trapped dust, the top of the bottle was inserted reverted and served as funnel with a 6 cm diameter. Before sealing the edges with a tape, a pre-weighed filter paper (each weighed after being dried for 12 h at 80 °C and numbered) was placed at the bottom to facilitate particle collection. Finally the traps were buried at two levels: 2 x 50 traps buried at ground level, and 2 x 50 traps buried so that the edge was ca. 2 cm above ground. This help to differentiate between sediment deposition from very local origin (sand particles of 10^{-1} – 1 mm) and sediment carried from greater distance (dust particles 10^{-3} - 10^{-2} mm). These particle sizes have three types of possible movements, which are defined as surface creep, suspension and saltation, the last are particles in motion that strike a hard surface. One needs to consider that particles produced by saltation can be deposited in both types of traps (Bagnold, 1954). The 100 bare terrain traps were spaced by 1 m; the 100 grassland traps were placed at 20 cm leeward distance of *Festuca orthophylla.* Exposure times were 36 h in the first series (summer) and 31 h the second time (winter). After the experiment, filters with sediments were dried at 60 °C during 3 days.

Data analysis

To compare the soil seed bank data between grassland and shrubland we used a nested analysis of variance, with the response variables; seed density and total seed weight per sample, and the categorical variable called cover with two levels grassland and shrubland, the factor nested is called microsite, with two levels, exposed and sheltered, there were 4 replicates. When the microsite differences were not significant we used one-way ANOVA to compare the seed density between grassland and shrubland. To analyse grassland seed bank response to grazing and fire, we also used a nested ANOVA with the fence as main treatment with two levels non-fenced and fenced, nested within the fire treatment and the control, the number of replicates was 4. Sediment test series data were studied individually by days, for the statistical analyses we used a two-way factorial ANOVA, the response variable was gm^{-2}, the factors were soil cover with two levels, uncovered and covered (*Festuca*) and the trap, also with two levels namely position, at soil level and above soil level. The statistical analysis was made with the free software R version 2.10.0 (www.cran.ch.r-projetct.org).

Results

Soil substrate characteristics

The Sajama's soil is mainly formed by sand of volcanic origin, which leads to rapid surface desiccation and moisture preservation in deeper layers (no capillary continuum). Soils in the 'pajonal' under *Festuca orthophylla* are slightly acid and under shrubland moderately acid (Table 1). In the uppermost 3 cm of the soil and at 10 cm depth, the electrical conductivity was low and raised with depth similarly in the two areas (Table 1).

Table 1. Chemical and physical soil characteristics

Vegetation	Depth cm	pH	CE ($\mu S\ cm^{-1}$)	Soil texture %		
				Clay	Silt	Sand
Pajonal	0-3	6.7	25.6	12	2	86
	10	6.5	92.0	18	2	80
Shrubland	0-3	5.6	40.2	19	3	78
	10	5.5	151.0	27	5	68

Composition of seed bank

The percent vegetation cover of the explored 'pajonal' area was 15.4 ± 6.6 (n = 4 plots) and for the shrubland 13.8 ± 6.1 (n = 4). The 'pajonal' and shrubland seed banks are mainly characterized by very small seeds (Table 2), with total seed counts set to 100%. The pajonal seed bank is formed by 3% *Festuca orthophylla*, 1% *Calycera*, 1% *Gamochaeta* and surprisingly, 90 % is made up from the 'bofedal' seeds species (not identified), brought by llamas and deposited in the soil through faeces, (Table 3). Intact seeds of the intra-tussock species *Senecio scorzonerifolius* seeds were absent in the seed bank. However the testa was present in several samples. In the shrubland 'bofedal' seeds again form 87% of the seed bank but the *Festuca orthophylla* fraction is much greater, 13% of all seeds. Hence we identified no seeds of the shrubs.

Table 2. Seeds characteristics, mean ± sd

Species (n)	Weight (mg)[a]	Length (mm)
Festuca orthophylla (11)	1.00 ± 0.29	4.05 ± 0.47
	0.49 ± 0.23[b]	2.99 ± 0.44
Calycera pulvinata (11)	1.98 ± 0.13 [c]	3.45 ± 0.43
	0.58 ± 0.13[d]	2.73 ± 0.23[d]
Mancoa hispida (17)	0.07 ± 0.02	0.63 ± 0.05
Tarasa tenella (16)	0.22 ± 0.07	1.16 ± 0.14
Deyeuxia sp.(sp1+awn) (12)	0.61 ± 0.13	20.03 ± 2.37
	-	(5.3 ± 0.02)[d]
Deyeuxia sp.(sp2) (15)	0.20 ± 0.06	2.11 ± 0.29
Senecio scorzonerifolius (19)	0.70 ± 0.09	3.76 ± 0.27
Gamochaeta sp. (14)	0.05 ± 0.02	0.99 ± 0.08
Gnaphalium (19)	0.03 ± 0.01	0.71 ± 0.12
Unknow 1 (29)	0.04 ± 0.02	0.42 ± 0.03
Unknow 2 (20)	0.12 ± 0.04	1.03 ± 0.10

[a] fresh weight full developed seeds
[b] without lemma ad palea
[c] seed + ripe fruit
[d] only seed
[e] without awn

Festuca orthophylla and *Calycera pulvinata* have the largest seeds in the seed bank. In average from the total seed weight of *Festuca* (Table 2) the lemma and palea (that remain attached to the seed) represent 50% of its weight, and for *Calycera* achene – like, ripe fruit represents 70% (Table 2). The two intra-tussock species *Senecio scorzonerifolius* and

Gamochaeta sp. with achene-pappus are poorly represented in the soil seed bank, *Senecio* is absent and *Gamochaeta* presence is extremely low.

Seed bank density in 'pajonal' vs. shrubland areas

Seed density in the 'pajonal' tended to be higher in the inter-tussock space than beneath tussocks. On the contrary seed density in the shrubland tended to be higher beneath shrubs than in the inter-shrub space. However, the 'pajonal' showed a higher seed density than the shrubland, none of these differences were significant (Fig.1). In terms of total seed biomass per square meter, there was significantly more seed biomass in the pajonal (*F=26.68; P=0.01*) than in the shrubland (Fig. 2), indicating that the grassland soil contained heavier seeds, but seed lots did not differ between microsites in either type of vegetation.

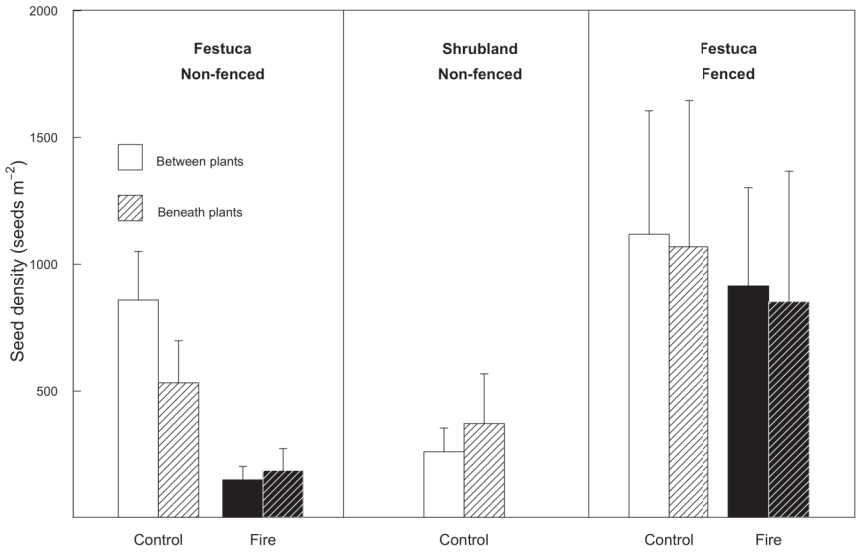

Figure 1. Soil seed bank density (mean + se, n=4) in *Festuca* grassland non-fenced and fenced control and fire. Shrubland soil seed bank only non-fenced control.

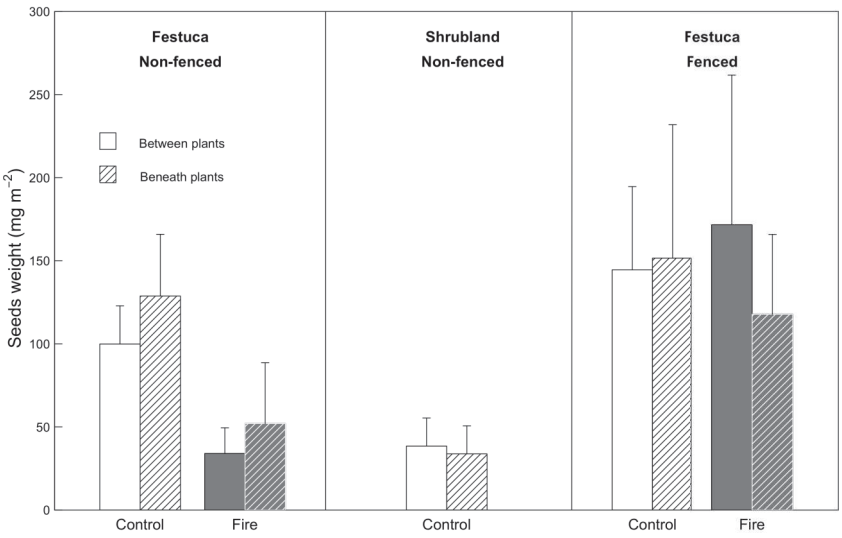

Figure 2. Seed biomass (mean + se, n=4).

Grazing and fire

The fence and fire interaction had a positive effect on seed density compared to non-fenced control and fire (*P=0.03*) Figure 1. Again there were no differences for microsites. In spite of the low seed density, the seed biomass per square meter was higher in the fire-fenced treatment than the control fenced and non-fenced control and fire, this difference was marginally significant (*P=0.07*). Overall there were very little seeds in the soil seed bank and those seeds belonged to 3 species of the local flora only. The biggest seeds fraction belonged to exotic seeds i.e. from the wet 'bofedal'.

Seed viability and vigour

From the total seeds in the shrubland, the percentages of viable seeds (red in TTC test) were lower in both microsites compared to the pajonal area (Table 3) but this difference was not significant. *Calycera* and *Festuca* exhibit the highest viability compared to 'bofedal' seeds, in spite of their low number (Table 3).

Wind speed and wind erosion

Wind velocity

The winds in the Altiplano are not considered strong, the monthly average of the maximum speeds ranging from 28 to 50 km h^{-1}, and monthly averages range from 8 to 19 km h^{-1}, in 2007

and 2008 (SENAHMI). We registered comparables wind velocities (Table 4) and a wind of 19.7 m s^{-1} (recorded in our experiment) may occur on 10 – 20 days per year, given that 16 days were recorded with the maxima 9 ms^{-1} in the campus of the Technical University of Oruro (more protected site). The grassland can reduce those maximal wind speeds by 62% compared to the bare soil area at 40 cm above soil.

Wind deflation

Sand and dust deflated by wind were significantly higher in the area without *Festuca* in all series (Fig 3. Table 4). The quantity of dust and sand deflated by saltation and suspension was in general lower than the amount of sand grains creeping on the soil surface (Fig. 3). Nevertheless, the presence of 15% land cover by *Festuca* can reduce the soil loss twofold for the medium and fine grains, and 6 fold for the coarse grains of sand (Fig 3 and 4). In spite of the fact that wind was not particularly strong during the test periods, a wind peak can considerable increase the total sediment transported in the bare soil area from 1 t ha^{-1} day^{-1} (produced on August 27) to 13 t ha^{-1} day^{-1} (August 29). During this last test alone 1.5 t ha^{-1} day^{-1} were removed (collected in the traps) in the pajonal.

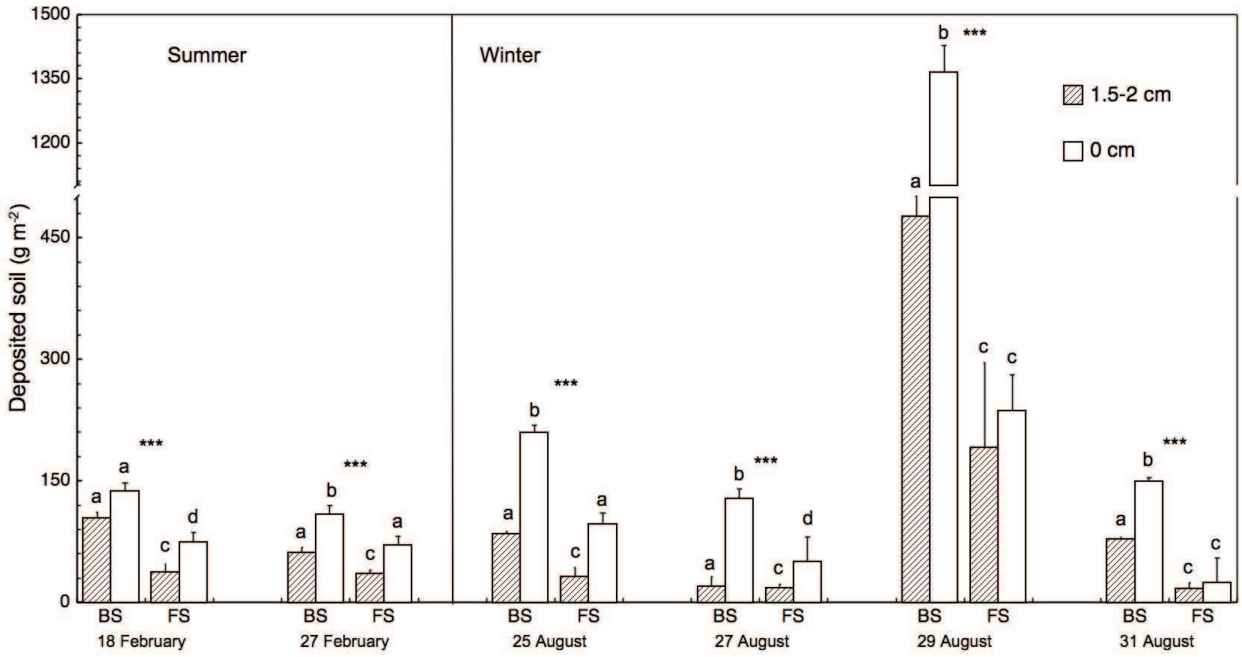

Figure 3. Soil erosion under different wind velocities (Table 4). BS = Bare soil; FS = *Festuca* covered soil. Stars mean significant differences between groups ANOVA. Different letters mean significant differences between means of above soil level and at soil level traps Tukey-test (0.05).

91% of all seeds found in the sediment traps were *Festuca* seeds, the remaining 9 % consisted of minor grasses and unidentified 'bofedal' seeds. There were no differences in the seed quantity transported with fine soil (dust, 2 cm aboveground) particles and coarse particles (ground-level traps). No seeds were trapped in the bare soil sediment traps, with the exception of the third series on 29th August, where 39% of the total seeds trapped on this date (mostly *Festuca*), were found in the bare soil traps, indicating that the dispersal of *Festuca* seeds is facilitated by the highest wind speed only. On the same date, sediment traps in the *Festuca* covered area trapped 61% of all seeds, indicating that the pajonal can retain a high seed fraction even during strongest winds.

Table 3. Total mean seed ± sd and percent of seed viability (%), in the pajonal and shrubland, (control n=4; fire n=4)

Treatment	Inter - plants				Beneath plants			
	Festuca	*Calycera*	*Gamochaeta*	Bofedal seeds	*Festuca*	*Calycera*	*Gamochaeta*	Bofedal seeds
'Pajonal'								
Non- fenced								
Control	0.1 ± 0.3 (100)	0.0 ± 0.0	0.1 ± 0.3	16.4 ± 4.9 (9)	0.6 ± 0.5 (80)	0.0 ± 0.0	0.0 ± 0.0	10.9 ± 7.8 (10)
Fire	0.5 ± 0.6 (50)	0.0 ± 0.0	0.3 ± 0.5	3.0 ± 1.7 (8)	0.8 ± 1.5 (100)	0.0 ± 0.0	0.5 ± 0.6	3.0 ± 4.1 (17)
Fenced								
Control	0.8 ± 0.6 (17)	1.1 ± 2.3 (78)	0.3 ± 0.5 (100)	21.0 ± 20.1 (7)	0.6 ± 0.5 (20)	0.0 ± 0.0	0.1 ± 0.3	25.9 ± 31.2 (10)
Fire	0.8 ± 1.0 (33)	0.3 ± 0.5 (100)	0.0 ± 0.0	20.0 ± 18.2 (9)	0.5 ± 0.6 (100)	0.0 ± 0.0	0.3 ± 0.5	12.3 ± 13.0
Shrubland								
Control	1.3 ± 1.9 (40)	0.0 ± 0.0	0.0 ± 0.0	6.5 ± 6.0	1.0 ± 1.4	0.0 ± 0.0	0.0 ± 0.0	8.0 ± 6.3 (3)

In parentheses, percentage values based in means of total viable seeds per treatment, no values means no viable seeds

Table 4. Wind velocity average means ± sd and absolute maximal wind speed in summer (rainy season) and winter (dry season)

Microsite	Anemometer position (cm)	Rainy season				Dry season							
		18 February		27 February		25 August		27 August		29 August		31 August	
		Abs. maximal	Wind average	Abs. maximal	Wind average	Abs. maximal	Wind average	Abs. maximal	Wind average	Abs. maximal	Wind average	Abs. maximal	Wind average
Bare soil	155	14.5	3.1 ± 0.6	14.9	3.9 ± 2.0	14.7	4.0 ± 1.7	9.6	0.9 ± 0.4	19.7	3.0 ± 1.5	11.8	2.1 ± 0.4
	75	13.3	1.8 ± 0.5	13.3	2.4 ± 2.1	-	-	-	-	-	-	-	-
	40	11.6	1.6 ± 0.5	11.9	2.2 ± 1.9	11.2	2.3 ± 2.0	9.1	0.4 ± 0.3	10.7	1.4 ± 0.8	9.1	0.6 ± 0.5
	10	8.3	0.9 ± 0.3	8.2	1.5 ± 1.3	-	-	-	-	-	-	-	-
Festuca	75	8.2	0.6 ± 0.4	9.0	1.1 ± 0.6								
leeward	40	5.9	0.1 ± 0.1	4.6	0.2 ± 0.3	7.0	0.3 ± 0.4	5.8	0.1 ± 0.1	10.6	0.1 ± 0.1	5.1	0 ± 0.1
	10	2.2	0.0 ± 0.0	2.5	0.0 ± 0.0								

Discussion

This study revealed a rather poor seed bank in the Altiplano tussock grassland and shrubland. The seed bank composition in semi-arid areas generally does not reflect the species composition of the area, in spite of that, our results show that the important species are present in the soil seed bank, but the overgrazing effect strongly diminished the seed density in the soil. Fencing showed that the seed bank could increase 1.5 times after two years without grazing disruption. A 15% land cover with *Festuca orthophylla* drastically reduced eolian sediment transfer. The movement of large quantities of the soilbed in bare areas due to the wind can drag seeds away. Our results show that grassland had a larger seed bank than the shrubland, on the contrary the Patagonian steppes' shrubs had a mean density of 1053 seeds m^{-2} and the scattered tussock patches 53 seeds m^{-2} (Aguiar et al. 1992).

The biggest and heaviest seeds had the highest vitality, *Festuca orthophylla* and *Calycera pulvinata*. These seeds had ticker coats than other species from the pajonal. Although size is not a universal predictor of seed longevity, morphological traits such as a hard seed coat are usually associated with longer-lived seeds (compared to soft-coated seeds; Chambers & MacMahom, 1994).

Seed density

The grassland seed bank density of 820 seeds m^{-2} (17% represent the persistent seed bank) was bigger compared to that reported for semi-arid South African grassland (58 seeds m^{-2}; Snyman 2005), but smaller compared to the central Andes of Chile 33° S, where a density of 899 seeds m^{-2} (persistent seed bank) was found for a percent cover vegetation of only 8% (Arroyo et al. 1999), or in the Patagonian grassland at 41° S, where the density was found varying from 906 to 2398 seeds m^{-2} due to drought (Gonzales & Ghermandi, 2008). The shrubland in our study area contains 382 seeds m^{-2} (inter shrub space) and 444 seeds m^{-2} (beneath shrub canopy) and is comparable to North American deserts (427 seeds m^{-2} reported by Guo et al., 1999). But the seed densities observed here are lower compared to the Bolivian prepuna's seed bank that ranges from 104 to 3846 seeds m^{-2} in the inter shrub space and 1767 to 2495 beneath shrub cover (Lopez, 2003).

Fire

According to Whelan (2001), a single fire may kill all the established plants in a population, but will release the seeds from the seed bank. If a second fire occurs after germination, this can be the critical one, and it has the potential to cause local extinction. In the Altiplano, fires do not occur subsequently. However, permanent trampling may avoid seedling establishment after fire.

Wind erosion

The wind peak of 68 km h^{-1} observed here at the end of winter was similar to what had been seen in the semi-arid pampa of Argentina (30°S), where the wind peaks between 50 - 60 km h^{-1} were found to cause a loss of sandy soil varying between 4 to 900 kg ha^{-1}, depending on plant residue coverage (Buschiazzo et al. 2007). In the sandy tropical soils of Nigeria, wind had been shown to mobilize 45 t ha^{-1} during four wind erosion events (Visser et al. 2004). In our study area, 59 t ha^{-1} were mobilized from bare soils, and 13 t ha^{-1} from *Festuca* covered soils, during four wind erosion events. *Festuca orthophylla* reduced soil transportation by around five times; also seeds are retained in the grassland during wind events. However, during extreme events, a substantial seed fraction can be transported to bare patches together with fine and coarse soil particles. This may open opportunities of re-colonization of bare soils, but intense trampling commonly avoids seedling establishment, as we observed in non-fenced burned areas. In the Patagonian *Festuca* grassland, where the annual mean of maximal wind speeds was 20.6 km h^{-1}, Defossé et al, (1997) found that bare patches caused by long-term ungulate grazing, can experience wind and water erosion that is detrimental for the survival of *Festuca* tussocks. A previous study in Sajama (Patty et al, unpublished data) showed a population reduction under grazing pressure. The current study confirms that grazing pressure does also reduce the seed bank. The study on wind dispersed forbs carried out by Soons & Heil (2002) showed that the capacity of plants to colonize new land decreased with decreasing plants population size in fragmented habitats. Also, the total (re)colonization capacity of the species is reduced, since the size of the seed bank is also reduced.

The Altiplano grassland soil seed bank reflects the situation of a highly disturbed ecosystem due to overgrazing and fire as the dominant land management practices, which also explain the extremely low biomass production of herbaceous species (Chap.3). In spite of grazing and fire, the fencing experiment showed the possibility of seed bank restoration. Fencing can also contribute to the re-colonization of bare soil areas by *Festuca*, thus leading to reduced erosion and an increase of important herbaceous fodder species, both, in the inter- and intra-tussock space.

Chapter 5

General summary

Summary

High mountain rangelands had been under human land use for millennia in most parts of the world. Traditional land care systems led to highly diverse and stable ecosystems. As these traditions fade and population pressure rises, these grassland systems become overgrazed, lose carrying capacity and biodiversity and become eroded. Semi-arid high elevation pastures in tropical and subtropical regions are particularly endangered. This PhD project aimed at assessing the plant inventory, the productivity and sensitivity of the herbaceous fraction of the flora to grazing by camelids in the *Festuca orthophylla* tall-tussock-dominated puna called 'pajonal' in the Bolivian Altiplano at 4250 m elevation (Sajama National Park 18°08'S, 68°58'W), with annual temperatures around 8.8 °C, the minimum and maximum temperatures were -5.9 and 31.0°C during the 2006-2008 observation period. This area receives between 250 and 350 mm of rainfall during a short (3-4 month) rainy season from December to March, this is also the growing season of the herbaceous species. The Sajama village has a population of about 150 families, with a long tradition in husbandry of llamas (53%), alpacas (39%) and sheep (8%).

My project was divided in three tasks, (1) a characterization of the herbaceous inter- and intra tussock flora, (2) a productivity assessment of the herbaceous pajonal components under various treatments, and (3) a study of soil seed banks and erodibility. The biology and productivity of *Festuca orthophylla* was investigated in a parallel PhD project (by José Monteiro).

(1) Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes

Besides developmental controls, assimilatory and respiratory processes as well as allocation of photo-assimilates to certain plant compartments are driving the rate of plant growth. These relationships are explored in what has been termed 'functional growth analysis'. Functional growth analysis considers (1) the relative amounts of dry matter invested in certain plant compartments and (2) the density and functional duration (amortization) of resultant tissues as the two major drivers of plant growth. While plant dry matter allocation is to a great part genetically determined for a given species, environmental influences can still cause significant shifts in investments towards needed structures. In this study we explored plant biomass allocation in perennial herbaceous plants growing in semi-arid, high elevation sites in the subtropical Andes. We hypothesized that under similar cold life conditions increased

herbivory pressure leads to more pronounced below-ground biomass allocation and that heavy camelid pressure with a cold climate and water shortage favours short rotation high N foliage. The study was carried out in two sites in the subtropical Andes which differed mainly in grazing pressure (higher in Bolivia) but were very similar in climate conditions: One in NW Argentina, Cumbres Calchaquíes, (26°40' S, 65°44' W). This high plateau at 4200-4600 m elevation receives on average 385 mm rainfall per year. The mean air temperature during the main growing season (November - March) is 4.5° C, and -1.6° C in winter, guanacos (wild camelids) represented the main grazers in this area. The other area (described above) the Sajama National Park area is under heavy grazing pressure, largely by llamas and alpacas, but also sheep and vicuñas. For our comparison we used three main biomass compartments: 'leaves', 'stem', and 'below-ground'; where 'stems' also include reproductive organs (mainly flowers), and 'below-ground' includes fine roots and storage organs.
The inter-tussock space in these open, dry plains ('pajonal') was dominated by rosette forming species with a below-ground shoot apex. We found less investment in leaves at these semi-arid sites as compared to other alpine regions, and a massive below-ground storage compartment (rhizomes, tap roots, 70% of all species), particularly at the colder Argentinean site, with a mean leaf mass fraction of only 11%. Though grazing pressure was much greater in Bolivia, the foliage mass fraction was larger than in Argentina. The storage organs of these species represented more than 50% of total biomass. In both areas the combined action of freezing conditions (down to -15.4 °C in Sajama) and grazing must have selected for these massive below ground structures, with a greater presumed effect of frost in the much colder site in Argentina and a greater presumed effect of grazing pressure in Bolivia.

Patty, L., Hiltbrunner, E., Körner, Ch. 2010. Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. Flora 205: 695-703

(2) Herbaceous species responses to grazing and fire in the Bolivian Altiplano

The semi-arid grassland of the Bolivian Altiplano is dominated by tall tussocks of *Festuca orthophylla,* the tiny, mostly perennial, herbaceous species are emerging during the rainy season only and represent high quality fodder due to their high leaf nitrogen concentrations and total non-structural carbohydrates (NSC). During the last decades, over-grazing (increase in livestock) and frequent burning have increased, with Bolivian stocks alone representing c. 63% of the South American llama population. The stocking density of llamas has gone up threefold in the last 20 years (fivefold in alpacas). This part of the project explores the

responses of these herbaceous species to grazing, fire and dung addition, in terms of diversity and productivity as well as forage quality (leaf N and NSC concentration).

In 2006, eight plots of 25 x 25 m were established (4 fenced and 4 unfenced) and the effects of fire (one initial burn in April 2006) and dung were tested in subplots (nested design). In this study we identified two types of non-tussock vegetation: the inter-tussock species mainly small rosettes and minor graminoids growing between *Festuca orthophylla* tussocks and the intra-tussock vegetation, growing inside tussocks.

Even after 3 years of animal exclosure, herbaceous species regeneration was minor, and there were only small absolute increases in productivity and diversity. The impact of grazing and associated trampling was far greater on these minor species as compared to *Festuca* tussocks. In 2007, a dry year, the aboveground biomass of inter-tussock species in unfenced plots was 20 mg m^{-2} and 500 mg m^{-2} in fenced plots; intra-tussock species in unfenced plots arrived at 30 mg m^{-2}, compared to 200 mg m^{-2} in fenced plots. In 2008, a more normal year, the biomass was higher, reaching 110 mg m^{-2} and 300 mg m^{-2} in unfenced and fenced inter-tussock vegetation, and 190 mg m^{-2} versus 500 mg m-2 in unfenced versus fenced intra-tussock plants. Dung addition without fence had no significant effect on herbaceous species, while the use of fire in unfenced areas suppressed the herbaceous vegetation. While fencing led to a clear biomass increase, other treatments only showed a positive response in the presence of the fence. Annual weather characteristics play an important role in plant species richness and composition. As the emergence of inter-tussock and intra-tussock species coincides with the camelids birth season; they can provide protein, sugar and starch, rapidly metabolized and likely to improve fat and milk production. Leaves of herbaceous species showed higher mean N (33 mg g^{-1} d.w.), and NSC (66 mg g^{-1} d.w.) concentration than *Festuca orthophylla* leaves (N 10 mg g^{-1} d.w.), and NSC 34 mg g^{-1} d.w. (data for n = 4 plots).

These results indicate that the current land management is highly deleterious for the most valuable fodder component of this ecosystem. Overstocking by llamas and intentionally set fires cause a massive decline in diversity and productivity of perennial herbs in this semi-arid grassland. Taking into account that future climate change may induce higher incidence of droughts in this region (IPCC 2007), we strongly recommend the periodic reduction of llamas livestock and banning intentional burning to facilitate regeneration of the non-tussock flora and maintain or enhance the carrying capacity of the land. Because *Festuca* tussocks do not cover the available canopy and rooting space, a large fraction of inter-tussock land remains unproductive and species poor, a niche that could be occupied by the non-tussock, ephemeral flora.

(3) Soil seed bank and wind erosion in the semi-arid Bolivian Altiplano

Soil seed banks have been studied because of their importance in ecosystem restoration, establishment and dynamics of vegetation succession. Several studies in semi-arid areas and deserts have shown great variability in the size and composition of seed banks, and fire and grazing can modify both, the size and composition of seed banks. In the Andes, the Altiplano soil seed bank is poorly known, but there is some evidence that the dry shrub puna offers favourable microhabitats for the establishment of a seed bank.

Grassland burning is still a common land management practice. After burning patches of bare soil are exposed during long periods to high wind velocity and drought. The preservation of a seed bank during and after wind erosion may help stabilizing the land during subsequent moist periods. In this study, I assessed the soil seed bank in the dry grassland (‘pajonal’) under the influence of tussock burning and grazing. Wind driven sediment deposition in those bare soil patches and seed translocation was explored for contrasting land cover by tussocks. The soil seed bank of adjacent shrubland was also studied for comparison. The study was conducted during the dry winter months, associated with strong and steady westerly and north-westerly winds over the entire region. The seed bank was assessed in the 8 test plots and simultaneously in four plots of 156 m^2 each in the shrubland next to the 'pajonal', to compare the seed quantities between open controls 'pajonal' versus grazed shrubland.

For the seed bank assessment, soil samples were collected with cores of 5 cm diameter at a 5cm depth, and eolian sedimentation was assessed with buried sediments traps. A vertical profile of local wind velocity was registered in open (bare) and tussock covered land.

The pajonal seed bank consisted of 3% *Festuca orthophylla*, 1% *Calycera*, 1% *Gamochaeta* and 90 % of all seeds came from the 'bofedal' terrain, brought in by llamas and deposited in the soil through faeces. In the shrubland around 87% of the seed bank is formed by 'bofedal' seeds and 13% by *Festuca orthophylla*. Although, the pajonal showed a higher seed density than the shrubland, the difference was not statistically significant due to the large variation. However, total seed biomass per square meter was significantly higher in the pajonal (*P=0.01*) than in the shrubland, meaning that the heaviest seeds stay in the grassland. In unfenced areas of the grassland, seed density was 860 seeds m^{-2} and in fenced plots 1120 seeds m^{-2}. The use of fire in unfenced areas drastically reduced the seed density to 150 seeds m^{-2}.

The reduction of tussock density as result of overgrazing enhanced the sediment deposition in traps by an equivalent of 59 t ha^{-1} during four extreme wind events (68 km h^{-1}). This quantity

would strongly increase on a longer time base, given that the number of extreme wind events is c. 10 to 20 day per year in the Altiplano.
It is concluded that the seed bank in the pajonal is extremely depauperate in local, adapted taxa, and the reduction of *Festuca orthophylla* tussock cover through overgrazing (trampling) and burning practices is increasing the eolian erosion and diminishes the herbaceous species diversity, recruitment and productivity in this area through negative effects on the seed bank. Given the poor seed bank and the high erodibility of the surface, a regeneration of inter tussock vegetation will profit from soil protection measures (e.g. mulch by lama dung), higher tussock density (better regeneration by periodic fencing) and amendments by sowing native species seed that could be produced in seed farms.

Overall this project revealed that the non-tussock flora is affected most heavily by land use and that a management for higher carrying capacity would also benefit biodiversity and fodder quality, while at the same time reducing eolian erosion. The management implications had been discussed with the local stakeholders and were well received. This Swiss funded project contributed a case study to the Global Mountain Biodiversity Assessment (GMBA) of DIVERSITAS (Spehn et al., 2006).

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Posters

Poster 1. International GMBA-DIVERSITAS conference "Functional significance of mountain biodiversity" Chandolin, Switzerland 2010

Poster 2. International conference: “Global Change and the World's Mountains” Perth, Scotland 2010

Poster 3. Towards sustainable land use in the Bolivian Altiplano, final results presentation
SNF-COSUDE project, and ALPANDINO course in La Paz, Bolivia 2011

Herbaceous species diversity in tall tussock grassland of the Bolivian Altiplano

Institute of Botany
University of Basel

Lita Patty, José Monteiro, Erika Hiltbrunner, Christian Körner

Introduction

Dry grassland 'pajonal' in the Altiplano is dominated by *Festuca orthophylla,* a perennial tussock with herbaceous species associated. Little is know about how does the herbaceous species respond to disturbance such as grazing and fire.

Objectives

- Analysis of plant biodiversity
- Herbaceous species productivity assessment
- Effects of grazing, fire and N addition on biodiversity
- Soil seed bank and soil protection

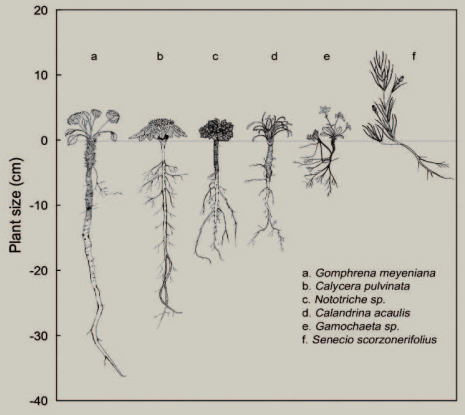

Fig. 1 Typical herbaceous species in the Bolivian Altiplano (Patty et al. Flora 2010)

Methods

The study was conducted in Sajama National Park, Bolivia, 4250 m (annual rainfall 350 mm).

- Eight 25x25 m parcels, four were fenced and four non-fenced and the effect of fire and dung was tested on subplots (nested).
- Seed bank evaluated collecting soil samples of 5 cm depth.
- Wind erosion assessment in bare and *Festuca* covered soil using traps and anemometers.

Results

- The herbaceous community is extremely sparse (<0.5 individuals m^{-2})
- Inter-tussock species mainly formed by rosettes (Fig. 1) and Intra-tussock perennial forbs are rich in N and NSC, compared to *Festuca* (Table 1)
- Fence enhanced biodiversity (Table 2)
- Fence increased seed bank 1120 vs. 860 seeds m^{-2} (Fig.2)
- *Festuca* tussocks reduced wind erosion (-62%; Fig.2)

Table 1. Leaf nitrogen and non-structural carbohydrates concentration

Species	N mg g^{-1}	C/N	NSC mg g^{-1}
Senecio scorzonerifolius	34.1	3	25.3
Gamochaeta sp.	24.7	17	54.3
Calycera pulvinata	43.4	10	68.9
Festuca orthophylla	10±1.2	48	34±0.6

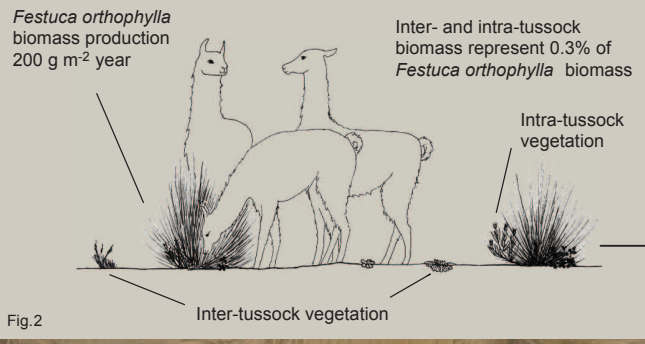

Fig.2

Table 2.

Herbaceous	2007		2008	
	Unfenced	Fenced	Unfenced	Fenced
Cover %	0.02	0.1	0.1	0.2
Shannon	0.02	0.3	0.4	0.6

Unfenced Unburned	Tussock land cover 15% reduces wind velocity 50%	Seed bank 860 seeds m^{-2}	Soil removed by wind 1.5 ton ha^{-1}
Unfenced Burned	Tussock land cover <0.5%	Seed bank 150 seeds m^{-2}	Soil removed by wind 13 ton ha^{-1}

Discussion

- Inter-tussock species have extremely low biomass production, but high nitrogen concentrations and non-structural carbohydrates.
- The emergence of inter- and intra-tussock species coincides with the camelid's birth season, they can provide protein, sugar and starch rapidly metabolized and available as fat and milk.
- The quantity and quality of seeds in the soil was found to be rather low, therefore not allowing fast regeneration.

Conclusion

Overgrazing and the use of fire as land management practice are causing a reduction in vegetation cover, which in turn increases the wind erosion and diminishes the plant species' diversity and productivity in this area.

Viola sp. | *Viola sp.* | *Gomphrena meyeniana* | *Nototriche sp.* | *Nototriche sp.* | *Nototriche turritella* | *Calycera pulvinata* | *Mancoa hispida* | *Senecio scorzonerifolius* | *Gamochaeta sp.*

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Efectos del pastoreo y la quema en la productividad de biomasa, diversidad y estabilidad del suelo en el altiplano boliviano

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Introducción

En las últimas décadas el sobre pastoreo y las quemas frecuentes han incrementado en el altiplano. Casi el 60 % de llamas de Sud América se encuentra en Bolivia. Los pastizales secos o pajonales en el altiplano están dominados por *Festuca orthophylla* (paja brava) donde se asocian pequeñas especies herbáceas ya sea entre plantas de *Festuca* o dentro de ellas. Este estudio explora las respuestas de estas herbáceas al pastoreo, adición de abono, a la quema y las respuestas de la biodiversidad, productividad y el banco de semillas del suelo. También exploramos la influencia de *Festuca* en el transporte de de suelo por el viento.

Métodos

El área de estudio fue el parque Nacional Sajama Bolivia, 4250 m (precipitación anual 350 mm)

- Ocho parcelas de 25x25 m cuatro cercadas, cuatro abiertas.
- Los tratamientos quema y adición de abono anidados en sub parcelas
- Evaluamos: la abundancia, biomasa, calidad de las herbáceas, banco de semillas y la erosión por el viento en suelo desnudo y cubierto por *Festuca*

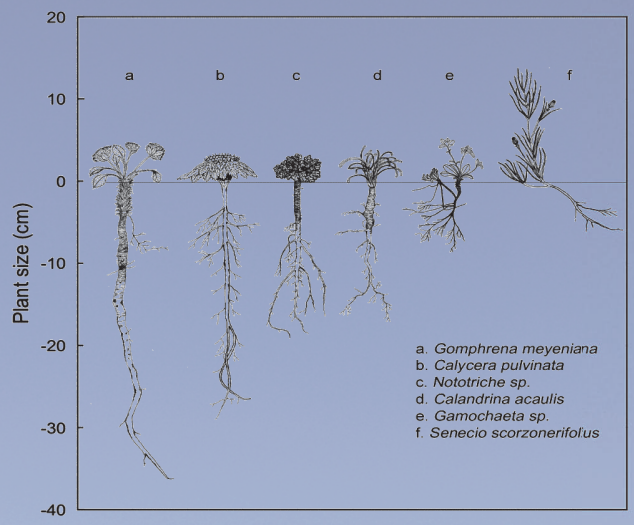


Fig. 1 Especies herbáceas características del altiplano boliviano (Patty et al. Flora 2010)

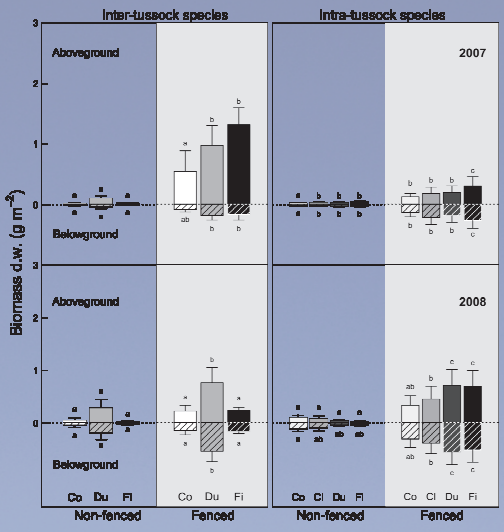


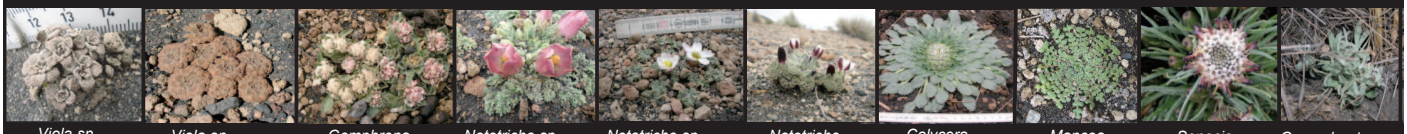
Fig. 2. Producción de biomasa peso seco inter-tussock é intra-tussock (medias + se). Diferencias entre cercado y no cercado *P<0.01* ANOVA para ambos años. Letras indican diferencia entre tratamientos test Tukey (0.05).

Tabla. 1. Riqueza, cobertura vegetal % , índice de Shannon o biodiversidad (medias ± sd). Shannon ligeramente alto en parcelas cercadas en 2008 (*P=0.05*, ANOVA). Cobertura vegetal incrementa en 2008 en parcelas abonadas

Parámetros medidos en control		No cercado	Cercado	*P*
Numero especies	(2007)	1.0 ± 0.8	2.0 ± 1.6	n.s
	(2008)	1.8 ± 1.5	3.0 ± 2.1	<0.01
Cobertura	(2007)	0.02 ± 0.03	0.15 ± 0.17	<0.05
	(2008)	0.10 ± 0.20	0.22 ± 0.23	<0.05
Índice Shannon	(2007)	0.08 ± 0.09	0.30 ± 0.34	n.s
	(2008)	0.35 ± 0.50	0.59 ± 0.40	<0.05
Abonado	(2008)	0.48 ± 0.69	1.40 ± 1.17	n.s.

Tabla. 2. Concentración de nitrógeno y carbohidratos no estructurales (NSC) en las hojas verdes de herbáceas comparadas con *Festuca*

Plantas	N (mg g^{-1})	C/N	NSC (mg g^{-1})
Senecio scorzonerifolius	34.1	3	25.3
Gamochaeta sp.	24.7	17	54.3
Calycera pulvinata	43.4	10	68.9
Festuca orthophylla	10 ± 1.2	48	34 ± 0.6



Viola sp. *Viola sp.* *Gomphrena meyeniana* *Nototriche sp.* *Nototriche sp.* *Nototriche turritella* *Calycera pulvinata* *Mancoa hispida* *Senecio scorzonerifolius* *Gamochaeta sp.*

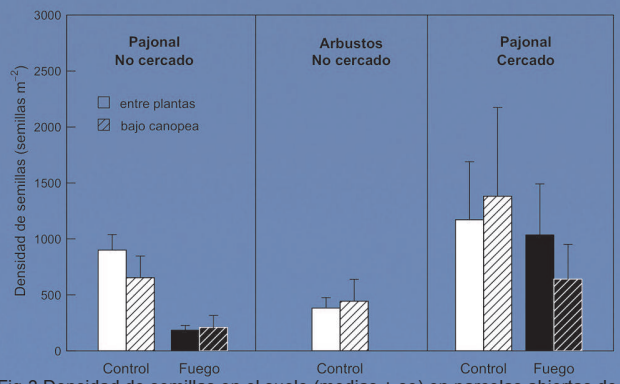


Fig.3 Densidad de semillas en el suelo (medias + se) en parcelas abiertas de *Festuca* y arbustos ns. Diferencia entre parcelas de *Festuca* abiertas y cerradas *P=0.03*, ANOVA

Vitalidad de las semillas

Jaborosa sp. *Calycera* sp. *Festuca* sp. no identificada

Fig. 4 Pigmentación del tejido vivo, prueba TTC. El color rojo muestra el tejido vivo de las semillas, la intensidad del color muestra el vigor de las semillas

Resultados

- La comunidad herbácea extremadamente dispersa (<0.5 individuos m^{-2}) y representa <1% de la producción de biomasa de *Festuca*
- Especies Inter-tussock principalmente rosetas (Fig.1), especies Intra-tussock son ricas en N y NSC, comparadas con *Festuca* (Tabla 2)
- La cerca incrementa la biodiversidad (Tabla 1)
- El tratamiento abono incrementa la cobertura vegetal (Tabla 1)
- La cerca incrementa el banco de semillas; 1120 vs. 860 semillas m^{-2} (Fig.3) en 5 primeros centímetros del suelo
- La viabilidad de semillas es baja, 5% en parcelas cercadas y no cercadas (Fig.4)
- *Festuca* reduce la erosión por viento del 53 - 83%, Fig.5)

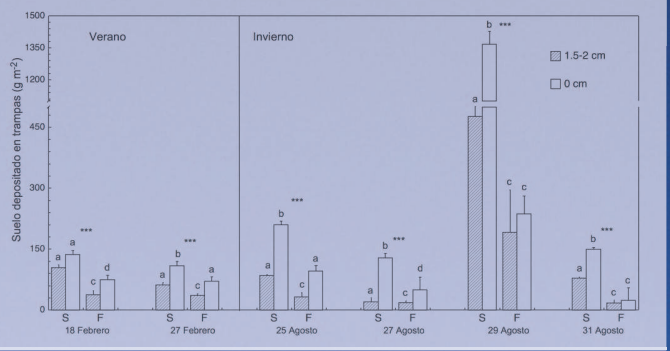


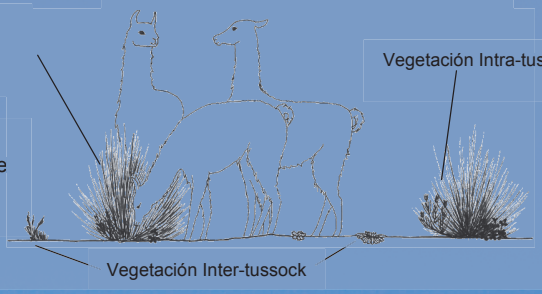
Fig. 5 Pérdida de suelo (medias + se) en S suelo desnudo y F con cobertura vegetal (Festuca 15 %). Las letras muestran diferencia entre grupos test Tukey (0.05), barras oscuras trampas sobre superficie del suelo, barras claras al nivel del suelo). Estrellas representan diferencia altamente significativa ANOVA en cada repetición entre suelo desnudo y cubierto

Demanda y oferta de proteína

1 llama adulta de 50 kg requiere 8.16 g N $día^{-1}$

Festuca orthophylla producción anual ~400 - 700 g m^{-2}

Biomasa de Inter- y intra-tussock representa <1% de biomasa de *Festuca orthophylla*



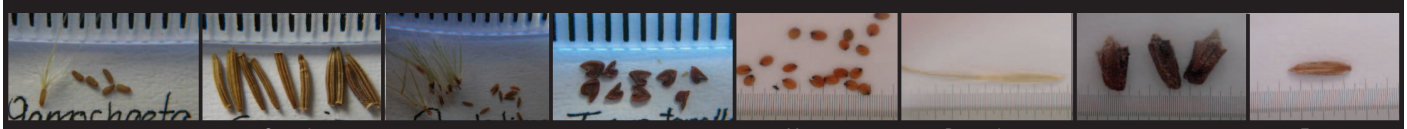
1 kg de *Festuca* 10 g N
1 llama adulta requiere 0.816 kg *Festuca* por día

Capacidad de carga recomendada por Alzérreca 2001 (0.4-0.5 llamas ha^{-1} $año^{-1}$)

1 kg herbáceas = 34.1 g N (promedio preferidas)
1 llama requiere 0.239 kg (8.16 g N) ~ 240 g
240 g $día^{-1}$ se producen en 60 ha (estado actual)
Considerando que un animal comería todas las plantas

Discusión y conclusión

- La producción de biomasa de las especies inter-tussock es extremadamente baja, pero su concentración de nitrógeno y carbohidratos no estructurales es muy alta.
- Las especies inter- é intra-tussock coinciden con la época de parición de camélidos, estas pueden proveer de proteína, azúcares y almidones rápidamente asimilables y disponibles como grasas y leche.
- La cantidad y calidad de semillas es muy baja y no permite una rápida regeneración.
- El sobre pastoreo y quema como prácticas de manejo del suelo están causando la reducción de la cobertura vegetal, que a su vez incrementa la erosión del suelo, disminuye la diversidad de las especies herbáceas y la productividad en esta área.
- Recomendamos evitar la quema y adaptar el número de animales a la capacidad de carga recomendada



Gamochaeta sp. | *Senecio scorzonerifolius* | *Gnaphalium sp.* | *Tarasa tenella* | *Mancoa hispida* | *Deyeuxia sp.* | *Calycera pulvinata* | *Festuca orthophylla*

Effects of grazing and fire on biomass productivity and diversity of herbaceous species in the Bolivian Altiplano

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Introduction

During the last decades over-grazing and frequent man-made fires have increased in the Altiplano. Bolivian stocks represents ca. 63% of the South American llama population. The dry grassland 'pajonal' in the Altiplano is dominated by *Festuca orthophylla,* a perennial tussock with small herbaceous species growing either within tussocks or in the inter-tussock space. This study explores the responses of these herbaceous species to grazing, dung addition and fire. We assessed biodiversity and productivity responses as well as the soil seed bank. We also explored the influence of tussocks on dust and seed translocation by wind.

Methods

The study was conducted in the semi-arid (350 mm a^{-1}) Sajama National Park, Bolivia 4250 m of elevation.
We used eight 25x25 m parcels, four fenced and four non-fenced fire and dung treatments nested in subplots.

Results

The biomass productivity is extremely low (<1 gm^{-2}, Fig. 1). and only represent <0.3% of *Festuca* biomass (Fig. 2). However, intra-tussock perennial forbs are much richer in N and NSC, compared to *Festuca* (Tab. 1). Fencing enhanced biodiversity (Tab. 2) and increased the size of the seed bank 860 vs 1120 seeds m^{-2} in the top 5 cm of the soil (Fig. 3). *Festuca* tussocks reduced wind speed -62% near the ground and erosion -80%

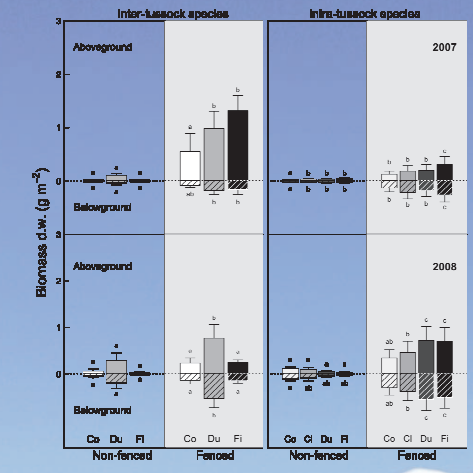

Fig 1. Herbaceous species biomass production (mean + se) on a dry matter basis for non-fenced and fenced treatments (n=4,). Significant differences (ANOVA) between non-fenced vs. fenced in both years (*P<0.01*). Different letters significantly different (Tukey HSD at 0.05)

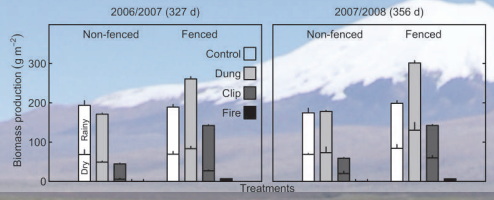

Fig 2. Biomass production for *Festuca orthophylla* in the Bolivian Altiplano (mean + se, n = 4 subplots, 6 plants per plot) for two years. Biomass production is divided for the dry and the rainy season (Monteiro, 2010).

Tab. 1. Leaf nitrogen and non-structural carbohydrates concentration NSC

Plant species	N (mg g^{-1})	C/N	NSC (mg g^{-1})
Senecio scorzonerifolius	34.1	3	25.3
Gamochaeta sp.	24.7	17	54.3
Calycera pulvinata	43.4	10	68.9
Festuca orthophylla	10 + 1.2	48	34 ± 0.6

Tab. 2. Diversity Shannon index and cover % (mean ± sd). Slightly difference for fenced plots in 2008 (*P=0.06*, ANOVA)

Herbaceous	2007		2008	
	Non-fenced	Fenced	Non-fenced	Fenced
Cover %	0.02 ± 0.02	0.1 ± 0.1	0.1 ± 0.2	0.2 ± 0.2
Shannon	0.02 ± 0.03	0.3 ± 0.3	0.4 ± 0.5	0.6 ± 0.4

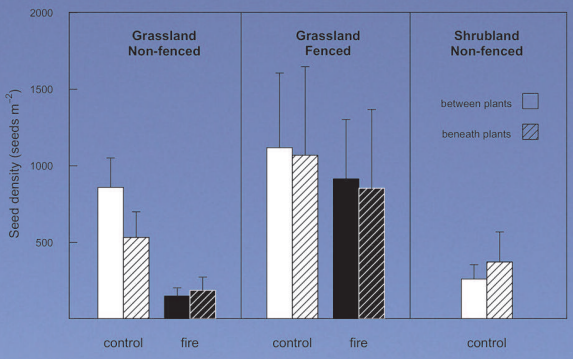

Fig.3 Soil seed density (mean + se) in non-fenced and fenced grassland and non-fenced shrubland plots (non-fenced vs. fenced grassland *p=0.03*, ANOVA).

Discussion

Land use pressure appears to suppress inter-tussock vegetation far more than tussocks. The emergence of inter- and intra-tussock species coincides with the camelid's birth season, they can provide protein, sugar and starch, rapidly metabolized and likely to improve nutrition.The quantity and quality of seeds in the soil was found to be rather low, therefore not allowing fast regeneration.

Conclusion

Overgrazing and the use of fire as land management are causing a reduction in herbaceous vegetation diversity, and thus, affecting the richest fodder component. The disturbance also reduce tussock density, leading to increases in wind erosion, further diminishing herbaceous plant species diversity, recruitment and productivity in this area.

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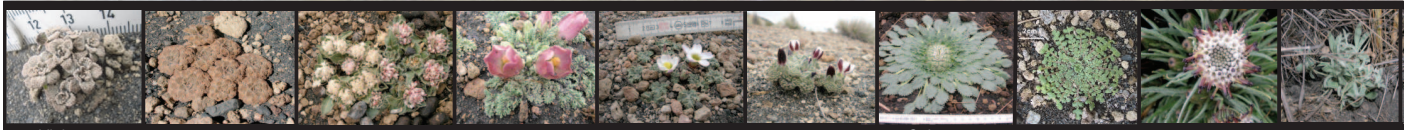

Viola sp. | *Viola sp.* | *Gomphrena meyeniana* | *Nototriche sp.* | *Nototriche sp.* | *Nototriche turritella* | *Calycera pulvinata* | *Mancoa hispida* | *Senecio scorzonerifolius* | *Gamochaeta sp.*

Annex

Scenario 1

1 adult llama (50 kg) needs 51 g protein per day or 8.16 g N day^{-1} (6.25 conversion factor)

1 kg *Festuca* dry matter contains 10 g N (lowest concentration).

1 llama needs 816 g *Festuca* d.m. (Considering only *Festuca* covering all N requirements)

Festuca production is 400 g d.m. m^{-2} a^{-1}, **if 10% is consumed by llamas** :

40 g d.m. m^{-2} a^{-1} / 365 days = 0.11 g d.m. m^{-2} day^{-1}

816 g d.m. *Festuca* day^{-1}/ 0.11 g m^{-2} day^{-1} = 7418 m^{-2} day^{-1} (0.74 ha day^{-1})

0.74 x 365 = 274 ha a^{-1}

1 llama / 0.74 ha day^{-1} = 1.3 llamas ha^{-1} day^{-1}

1 llama / 274 ha a^{-1} = 0.004 llamas ha a^{-1}

Scenario 2

According to Genin 1994 (and other authors) *Festuca* represent 20 – 41% of llamas diet.

Considering that 40 % of llamas' diet is *Festuca*, then:

1 llama consumes 326 g d.m. *Festuca* (**40%** of 816 g)

326 g d.m. *Festuca* day^{-1}

Festuca production is 400 g d.m. m^{-2} a^{-1}, **if 10% is consumed by llamas** :

40 g m^{-2} a^{-1} / 365 days = 0.11 g m^{-2} day^{-1}

326 g d.m. *Festuca* day^{-1}/ 0.11 g m^{-2} day^{-1} = 2967 m^{-2} day^{-1} (0.3 ha day^{-1})

0.3 x 365 = 109 ha a^{-1}

1 llama / 0.3 ha day^{-1} = 3.3 llamas ha^{-1} day^{-1}

1 llama / 109 ha a^{-1} = 0.009 llamas ha a^{-1}

Colour plates

Viola sp.

Calycera pulvinata

Deyeuxia sp.

Gamochaeta sp.

Nototriche sajamensis

Mancoa hispida

Senecio dryophyllus

Tarasa tenella

Perezia carduncelloides

Nototriche pulverulenta

Calandrina acaulis

Lupinus chilensis

Gomphrena meyeniana

Senecio scorzonerifolius

Nototriche turritella

Gnaphalium sp.

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Education

2007-2011 Doctoral student at the Botanical Institute – Basel University
Project title: *Towards sustainable land use of the Bolivian Altiplano: Effects of grazing and fire on biomass productivity, diversity and soil stability*

2005-2007 Diploma in International Environmental Laws – United Nations environment program UNITAR.
Memoire title: *Pollution transfrontière de la rivière Pilcomayo – Evaluation de l'état actuel des négotiations entre la Bolivie, l'Argentine et le Paraguay*

2003-2005 Postgraduate studies at the EPFL: Master of Advanced Studies in Environment, Sciences, Engineering and Management.
Postgraduate Thesis: *Physicochemical quality of deadwood (Picea abies) in the protected forest of Montricher (VD), Switzerland*

1995-2002 Title of Engineer in Agronomy at the – Universidad Mayor de San Simón (UMSS), Cochabamba – Bolivia.
Diploma Thesis: *Evaluation of protected areas management efficiency: Case National Park Tunari. Cochabamba-Bolivia*.

1991 Secondary School Magdalena Postel, Oruro – Bolivia.

Professional Experience

2005 Three months internship at the GECOS laboratory (EPFL), to prepare a scientific paper based on my postgraduate thesis.

2003 Training in: Industrial Environmental Inscription – Environmental Unit of the Vice-Ministry of Industry, Commerce & Exportations and the Danish Environmental Cooperation Programme, Oruro – Bolivia.

2002-2003 Environmental control project leader for the installation of natural gas at INDELGAS (Engineering of Gas), Oruro – Bolivia.

2001-2002 Research Assistant for *Project IV, 16 Program CYTED (Sciences and Technology for the Development): Added Value for the Euphorbiaceae and Leguminosaceae Waste of the American Forest* – Cochabamba - Bolivia.

Publications

Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. Science Direct – Flora 2010.

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